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The Bionomics of a Primitively Social Bee, *Lasioglossum inconspicuum*¹

BY

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ABSTRACT: *Lasioglossum inconspicuum* is a common small halictid bee in eastern North America. It nests solitarily or in loose aggregations. The nests are in the ground, in sunny areas of bare soil. The burrows are deep, more or less vertical, with subhorizontal cells along them (Figures 5 to 16). This species visits a wide variety of flowers (Table I) but largely ignores the extensive flora of yellow autumnal Compositae. Afternoon activity on flowers is markedly less than that in the morning, and a much smaller percentage of the bees that are afield collect pollen in the afternoon than in the morning. A brief midday drop in activity is indicated by the observations (Figure 1).

Overwintering occurs as fecundated queens in the nests used the previous season; these queens begin spring activities in late March or April. Most of them establish new nests as lone individuals but some remain in the overwintering nests. Sometimes as many as six queens or potential queens may jointly occupy an old nest. There is evidence that in such cases some of them sometimes have a workerlike rather than egg-laying function. The mortality of colonies is very high throughout the season (Figure 4) but the reasons for the high mortality are not clear.

The queen nests, whose cells are provisioned by queens in the spring, become closed in May and are reopened by emerging workers at the end of May or in early June. The nests are then enlarged, a process which goes on (if the colony survives) through the summer. The queen lays more eggs as cells are completed and provisioned during the summer. During this time the queens do not leave the nests with the frequency of workers, but possibly do so less frequently to feed. They do not collect pollen. Their mandibles, however, become progressively more worn, indicating that they work in the nest. Some queens die during the summer and are seemingly replaced by young females. Such replacement queens do not survive the following winter.

Workers, in contrast to queens, are quite short lived, surviving as adults for perhaps three weeks. Some workers have one or even two ovarioles enlarged and presumably lay a few eggs (Figure 28). Such egg-laying workers collect

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pollen freely and seem to act otherwise like typical workers. Young workers act as guards and become lost if removed from the nest. Older workers do the foraging except in spring when the queens are establishing their colonies. The number of foraging trips per unit time varies greatly (Table II), as does the duration of such trips (Figure 3).

Males are absent in the first broods produced by overwintered queens but appear in small numbers in June, much larger numbers in August and early September (Figure 22).

The average number of females in a colony varies seasonally as shown in Figure 21; there is very wide individual variation in colony size as shown in Table VII.

Workers average smaller than queens (Figure 31), but in some nests the largest worker is larger than the queen. Egg-laying workers average larger than those with slender ovaries, but smaller than queens. The mean size of workers in July is smaller than in June or August. A similar seasonal fluctuation in size of males was noted (Figure 23).

There is no evidence of communication among individuals of a colony. The return of a forager does not seem to constitute a stimulus for other foragers to leave the nest. The guards seem quite unable to distinguish individuals of their own colony from those from other colonies. Young workers that have not yet been afield and learned the location of their own nest can be transferred to another nest where they soon function as guards and live out their lives, their alien origin apparently not recognized. Workers that are older, if transferred to another nest, soon leave it and return to their own nest.

CONTENTS

	PAGE
INTRODUCTION	1125
GENERAL ACCOUNT OF LASIOGLOSSUM INCONSPICUUM	1127
Distribution	1127
Life History	1128
Seasonal Cycle	1128
Natural Enemies	1129
ACTIVITY OUTSIDE THE NESTS	1130
Conditions for Outside Activity	1130
Hours of Activity	1130
Flowers Visited	1132
Methods of Foraging	1133
Activity Around the Nests	1134
Duration of Trips and Periods Between Them	1137
Probable Lack of Social Facilitation	1140
Length of Flights	1143
NESTS	1143
Distribution of Nests	1143
Common Features of Nesting Areas	1147
Differences in Activities Among Nesting Areas	1148
Survival of Nesting Aggregations	1149
Survival of Nests	1150
Nest Structure	1151
Nest Construction	1161
Provisions and Immature Stages	1163

	PAGE
INDIVIDUAL AND SOCIAL BEHAVIOR	1165
Aggregations of Nests	1165
Nest Populations	1166
Males	1167
Variation in Size Among Field-collected Females	1171
Caste Differences	1171
Seasonal Differences in Size	1179
Queens	1182
Workers	1187
Behavior of Queens	1190
Division of Labor Among Queens in Polygynous Nests	1192
Behavior of Workers	1193
Guarding and Other Activities at the Nest Entrance	1194
Co-operative Activity Among Workers	1198
NEED FOR FURTHER STUDY	1199
LITERATURE CITED	1201

INTRODUCTION

This paper provides an account of the life cycle and behavior of one of the primitively social halictine bees, *Lasioglossum (Chloralictus) inconspicuum* (Smith). This study is part of an investigation of comparative halictine behavior intended to shed light on the origin and evolution of social behavior and castes. Observations were made over a period of eight years in the vicinity of Lawrence, Kansas. During several of those years efforts were made to follow the life cycle as completely as possible; during other years our efforts were directed toward elucidation of certain details of the life cycle or behavior. The methods used are largely those described by Linsley, MacSwain and Smith (1952) and by Michener, Cross, Daly, Rettenmeyer and Wille (1955), although many of them are further explained in appropriate places below.

Over 200 nests were excavated and 929 females were dissected to determine the condition of the ovaries, spermatheca, and crop, examined to determine mandibular wear and measured to determine size. Hundreds of other observations on living marked and unmarked bees were made, so that for example, we have about 125 records of the duration of pollen collecting flights of individual females.

Probably a majority of the species of the enormous subfamily Halictinae are social to a greater or lesser degree. The several bees inhabiting a single nest are said to constitute a *colony*; groups of nests placed close to another another constitute an *aggregation*. Since social behavior evidently arose repeatedly and independently

in various evolutionary lines within the subfamily, this group offers unparalleled opportunities to investigate incipient and primitive societies. A synthesis of the available information on halictine behavior and evolution will be presented later. It will suffice here to give a brief account of previous works on the biology of the subgenus *Chloralictus*¹. *L. opacum* (Moure) from Brazil appears to be a solitary bee without strong aggregative tendencies and without a worker caste (Michener and Lange, 1958). Presumably males and females appear in roughly equal numbers throughout the season.

In *L. rhytidophorum* (Moure) (see Michener and Lange, 1958) and probably in *L. seabrai* (Moure) and *guaruvae* (Moure) (see Michener and Seabra, 1959), small colonies exist in which there are weakly differentiated queens and workers. At least in *rhytidophorum* the queens, of which there are usually two or more per nest, are rather frequently replaced and males are produced throughout the reproductive season, although in smaller numbers in summer than in spring and fall. In *L. inconspicuum* the colonies are larger, there is more often only one queen in a nest, more workers are produced per queen, workers and queens are a little better differentiated, and queens probably often survive for most of a year. Males are not or scarcely produced early in the reproductive season (spring and early summer), appear only in moderate numbers in midsummer, but become abundant in the autumn.

The nest architecture is known for more species of *Chloralictus*. In addition to those listed above it is known for *L. pruinatum* (Robertson) (see Melander and Brues, 1903), *rohweri* (Ellis) (see Sakagami and Michener, in press), *smilacinae* (Robertson) (see Brittain, 1933), *versatum* (Robertson) (see Sakagami and Michener, in press), *zephyrum* (Smith) (see Sakagami and Michener, in press) and for perhaps half a dozen unidentified species. In all of these the nests are similar, each consisting of a branching main burrow from which diverge subhorizontal, bilaterally symmetrical, wax lined cells connected to the main burrow without or by very short lateral burrows. Only in *L. aricense* (Schrottky) (= *Halictus glabriventris* Friese) and *herbstiellum* (Friese) (see Claude-Joseph, 1926) from Chile are the basic features of the nest architecture different from that of the above species. Possibly these forms are not properly included in *Chloralictus*, or perhaps they were misidentified by Claude-Joseph.

A small amount of information on nests and behavior of *L. in-*

1. Australian species included in *Chloralictus* by Rayment in various publications treating of biology are in reality not related to *Chloralictus*.

conspicuum is found in the papers by Michener, Cross, Daly, Rettenmeyer and Wille (1955), Michener (1958), and Michener and Lange (1958). In these publications the synonymous name, *stultum* Cresson, is used for this species. The meager conclusions on this species presented in those papers appear in greater detail in the present work.

We wish to acknowledge grants from the National Science Foundation which made the study possible. We wish also to thank several persons who helped with the field observations. This has been no light task, as those who have spent long hours on the ground watching or digging bees' nests in the hot summer sun can testify. The persons concerned are Earle A. Cross (now of Northwestern State College, Natchitoches, Louisiana), Howell V. Daly (now of the University of California, Berkeley, California), Wallace E. La Berge (now of the University of Nebraska, Lincoln, Nebraska), Ellen Ordway of the University of Kansas, Carl W. Rettenmeyer (now of Kansas State University, Manhattan, Kansas), and Alvin F. Shinn (now of Stephen F. Austin State College, Nacogdoches, Texas).

Dr. David S. Simonett of the Department of Geography, The University of Kansas, kindly visited the main nesting sites and provided the data on soils.

The statistical analyses were done by Miss Ellen Ordway with guidance from Gunther Schlager and F. James Rohlf.

GENERAL ACCOUNT OF LASIOGLOSSUM INCONSPICUUM

Distribution: This minute greenish black bee, nearly 4 to nearly 5 mm. in length, is widespread over eastern North America, occurring from Quebec to Georgia, westward to Wisconsin, New Mexico, and Texas (Michener, 1951). Over much of this area it is one of the commonest native bees, although so inconspicuous that it is often unnoticed even by entomologists. The species also occurs in the vicinity of Riverside, California, where it was presumably introduced from the eastern or central part of the United States.

In eastern Kansas, where our observations were made, the species is generally distributed. It is sometimes very common and can be taken at least occasionally on almost any clump of suitable flowers. In this area trees and bushes cover most of the noncultivated terrain and the average rainfall is relatively high (35 inches annually at Lawrence). In central Kansas (area of Caldwell, Hutchinson, and Salina), however, the rainfall is less and uncultivated land is largely treeless except in stream valleys. In this area *L. in-*

conspicuum is largely confined to stream valleys although other species of its subgenus are common in the drier uplands.

Although *Lasioglossum inconspicuum* is found in an area most of which was once deciduous forest, it is not a bee of forests themselves. It usually nests in exposed bare soil, as will be discussed in detail in the section on "Distribution of Nests," and we have never found it burrowing in the forest floor. Originally the forest margins and perhaps occasional bare streamside areas must have been its chief habitats. Destruction of forests, overgrazing of pastures, erosion of soil and development of brushy or weedy wastelands must have enabled the species to become much more abundant and possibly more widespread than in primeval times.

Life History: A brief account of the life history of *L. inconspicuum* is given here to provide background for subsequent sections of the paper, where most of the matters mentioned will be treated in greater detail. The bee is social to the extent that its nests, which are burrows in the soil, are usually occupied by several females. One or more of these is a queen, the others workers, but these castes are very similar and overlap broadly in size. Without information as to season, young females can be placed as to caste only if unusually small (workers) or large (queens). The caste of older individuals (with worn mandibles) can be determined more readily when ovarian development and spermathecal contents are considered.

The species overwinters as adult fertilized queens in the nests. In the spring these queens provision cells and lay eggs, either in new nests or in the old ones. The cells are mass provisioned and usually closed after the eggs are laid, as in most other halictines. After preparing about five cells, the queen ceases her activities until these progeny reach maturity. All of them are workers. They deepen the nest and provision other cells in each of which the queen lays an egg. From this time on the nest is usually continually active, there being no separated broods as in the European *L. malachurum*. The short-lived workers are replaced as they die so that several of them are ordinarily present in the nest. The queens probably are sometimes replaced during the summer, and some males are produced during that season. In fall queens and males are produced in the nests, and it is these young queens which pass the winter.

*Seasonal Cycle*¹: Overwintered queens were first seen in the

1. Numbers in parentheses in this section indicate the number of years when appropriate observations were made.

spring at Lawrence, Kansas, on various dates from March 25 to April 16(6). Three of the six early spring records are in the first week of April. Each of the early records is based on an observation of bees flying about or alighting on the ground, but without any evidence of excavation of cells or other work in the nest. Tumuli (piles of excavated earth) at the nest entrances or regular going in and out of well rounded nest entrances were first noted on dates ranging from April 3 to 26(6). The first queen seen carrying a pollen load into the nest (*i. e.*, the first evidence of provisioning of cells) was observed on dates ranging from April 13 to May 1(7).

The first bees recognized as workers, either by dissection or by augmentation of nest populations, were noted on dates ranging from May 31 to June 10(5). Males were first seen, always in small numbers (usually only one or two in hours or days of observation), on dates ranging from June 1 to June 18(5). Because males might be produced as a sort of abnormality in nests that had lost their queens, and because the records in the first half of June may represent the parasitic species, *Lasioglossum cephalotes*, it seems worth noting that our earliest excavations of male pupae from nests which also contained female pupae were from June 20 to July 8(3). Since we dug relatively few nests, about 40 during June, compared to the total numbers of nests in the areas studied, it is not surprising that males from one or another nest would be seen in flight before any male pupae were found in nests. We therefore cannot be sure of the significance of the late dates for the male pupae. We did dig one nest containing male but no female pupae on June 17.

The last females, presumably workers, were seen carrying pollen on dates ranging from August 28 to September 13(4) and very few cells are provisioned as late as these dates. The last overwintering queens were seen in flight from October 1 to 22(4); the last males from September 26 to October 12(3). Overwintering queens were seen guarding nest entrances as late as October 10 to 22(3).

Natural Enemies: *Lasioglossum (Chloralictus) inconspicuum* is frequently parasitized by *L. (Paralictus) cephalotes* (Dalla Torre). A later paper will concern the biology of this parasitic species and its relations to its various hosts, all of which are in the subgenus *Chloralictus*.

A small mutillid, *Pseudomethoca frigida frigida* (Smith) (det. K. V. Krombein) is common in and about the nests of *L. inconspicuum*. It has not actually been reared from cells of this bee. [We have also taken it in the nests of *Lasioglossum zephyrum*

(Smith), *rohweri* (Ellis), and *versatum* (Robertson) and in nests of *Augochlorella striata* (Provancher).]

We have reared males of a minute tiphiid, *Myromosula parvula* (Fox) (det. K. V. Krombein), from their cocoons in cells of *L. inconspicuum* and have captured a few females in the nests of the *Lasioglossum*.

Female (but not male) Strepsiptera (*Halictoxenos*) are occasionally found in abdomens of *L. inconspicuum*, as are larvae which appear to belong to the Conopidae (Diptera).

Except for the forms listed above, natural enemies in nest of *L. inconspicuum* are not noticeable. Some cells are destroyed by mold, but there is always a question as to whether this is a primary enemy or merely attacks already dead eggs or larvae, thence spreading onto the pollen mass.

Outside the nests, of course the adults are subject to the usual predators.

ACTIVITY OUTSIDE THE NESTS

Conditions for Outside Activity: Detailed data on temperature, light, wind, and other factors associated with flights from the nest have not been obtained, as other data seemed more important. However, the meager information obtained is perhaps worth recording. Except as otherwise indicated, temperatures were taken in the shade of the observer's body 30 cm. above the ground. At 50° F. no bees were seen. At 62° F. guards were seen in some nests, but no flights were made. Pollen-collecting flights were observed at temperatures ranging from 70° to 105° F. Of course temperatures at the soil surface are much higher in direct sun light, and as will be explained in more detail in the section on "Guards," the guards withdraw from unshaded nest entrances when the temperature obtained by laying a thermometer on the ground surface in direct sun light reaches about 125° F.

Of course strong wind usually results in reduced activity, but pollen collecting flights sometimes occur when a warm wind is blowing so strongly that the bees are rolled over and over on the ground if they alight in approaching the nest. At such times bees may cling to weeds and leaves, and several may then enter a nest in quick succession when there is a lull in the wind.

Hours of Activity: The time of day when activity begins varies with the season. On various clear days in June, the first flights from nests in the morning were observed from 6:40 a. m. to 9:00 a. m.; on

cloudy days the first flights were later. In the afternoon, a bee was seen to leave the nest as late as 4:55 p. m.

It is a common observation of persons collecting bees about flowers that, except on the hottest days, collecting is best in late morning hours. As a biproduct of observations of the activities of marked bees, we obtained numerical verification of this collector's impression. Figure 1 shows the number of worker bees entering at different times of the day into nests that were under observations. The maximum was reached during the period from 8:30 to 11:30. Our data were largely gathered during hot summer days; this may explain the relatively early maximum. Afternoon activity was about half of that in the morning. Separate lines for bees returning to the

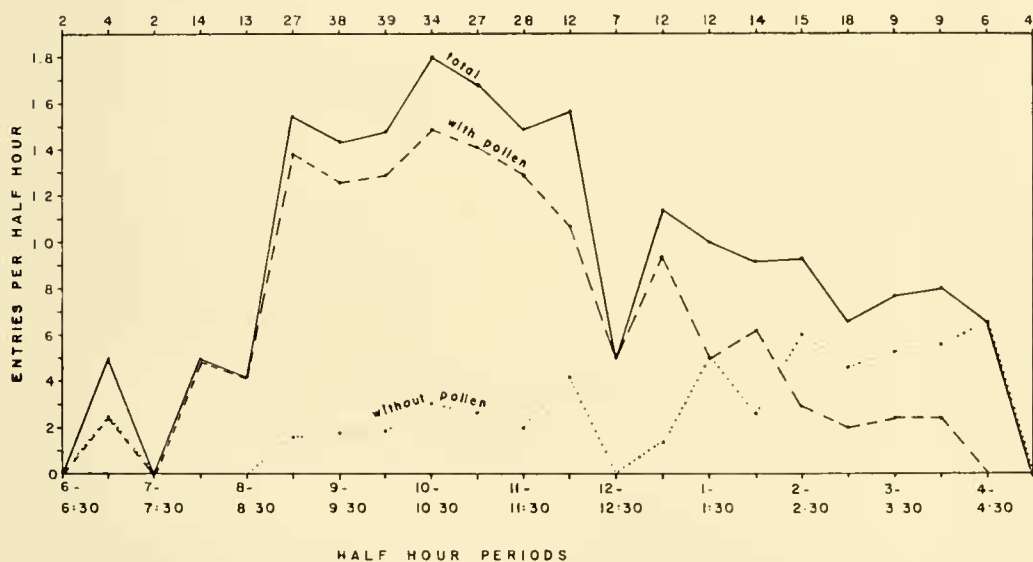


FIGURE 1. Graph showing the average number of times per half hour period that females (probably all workers) entered their nests after trips afield. All observations were made during the months of June, July, and August. The figures across the top of the graph show the number of half-hour periods during which nests were under observation; irregularities in the early morning are doubtless due to the small number of observations. The *solid line* indicates the total average number of entries. The nests studied were usually the most active ones available, so that the figures are strongly biased upward. The *broken line* shows the average number of entries of bees with pollen loads on the legs. The *dotted line* shows the average number of entries of bees without pollen loads. The total is sometimes higher than the sum of the other two, since bees sometimes got into their nests without our determining whether or not they were carrying pollen.

nest with and without pollen loads on the scopa show pollen collecting to be the dominant outside activity in mornings but flights presumably for nectar gathering or probably merely for feeding of adults increase through the day (except for a midday lull) and are the dominant outside activity in late afternoon. We know from observations of bees marked for individual recognition that at least

some of the afternoon flights from which bees returned with no pollen loads were made by individuals which had collected pollen earlier in the day and did so also the next day.

There is no reason to believe that the reduced afternoon activity is due to poorer weather in the afternoon. The observations were made during 50 different days scattered through three summers. The reduced activity may be related to reduced availability of pollen because it is utilized by bees during the day, but some individuals were able to obtain pollen loads in short periods of time in the afternoon and the average duration of pollen-collecting trips was not longer in the afternoons than in the mornings. It seems likely that an innate feature common to the activity of most bees is the tendency, in fine weather, to do more foraging in the mornings than in the afternoon. Scattered data on other species suggests that the afternoon increase in trips for purposes other than collecting pollen is also a common tendency at least among halictines.

Flowers Visited: Like most halictines, *Lasioglossum inconspicuum* is polylectic, that is, it visits and even collects pollen from a wide variety of flowers. Polylecty is a usual characteristic of social bees; since such bees are active through a long season, no one flower is ordinarily available to them at all seasons. No serious effort was made to obtain a comprehensive list of kinds of flowers visited by *L. inconspicuum*, since it was felt that almost any flower visited by any bees in our area would be visited at least occasionally by this species. Table I was based upon data on specimens in the Snow Entomological Museum as well as on observations made in the course of the study of this species. Except as otherwise indicated, females or both sexes were found on flowers in the list.

Examination of Table I shows that the large yellow-flowered Compositae (*e. g.*, *Helianthus*, *Silphium*) so conspicuous in late summer in Kansas are little visited by *L. inconspicuum*, although many other bees, including other species of the subgenus *Chloralictus*, regularly visit these flowers. The selection of flowers is similar to, although more catholic than, that of *Megachile brevis* Cresson (see Michener, 1953) which also uses primarily blue to whitish flowers. *L. inconspicuum* sometimes collects pollen from yellow flowers of *Taraxacum officinale* in the early spring, possibly because there is sometimes a shortage of other flowers at that season.

It is apparent that even in a species of seemingly thoroughly polylectic bee, by no means all of the potential pollen and nectar sources are used. Expressed in different terms, the bees seem to

TABLE I.—List of Flowers on which *Lasioglossum inconspicuum* Has Been Taken in Eastern Kansas. P indicates that females were collecting pollen, S that they were sucking nectar but not collecting pollen. We have no notes concerning activities of bees on flowers not marked either P or S.

Liliaceae		Malvaceae	
<i>Allium</i> sp.		<i>Callirhoe digitata</i>	
Gramineae		Lythraceae	
Unidentified	P	<i>Lythrum alatum</i>	P
Cruciferae		Umbelliferae	
<i>Sisymbrium</i> sp.?		<i>Daucus carota</i>	
Roseceae		Asclepiadaceae	
<i>Spirea vanhouttei</i>	P	<i>Asclepias tuberosa</i>	S
<i>Prunus americana</i>	P		
<i>Fragaria virginiana</i>		Labiatae	
<i>Malus pumila</i>		<i>Monarda fistulosa</i>	P
Leguminosae		Plantaginaceae	
<i>Petalostemon candidum</i>		<i>Plantago rugelii</i>	P
<i>Psoralea floribunda</i>	(♂)	Compositae	
<i>Melilotus officinalis</i>	S	<i>Taraxacum officinale</i>	P
<i>Melilotus alba</i>	P	<i>Silphium speciosum</i>	S
<i>Medicago sativa</i>	P	<i>Silphium perfoliatum</i>	
<i>Cercis canadensis</i>	P	<i>Solidago</i> sp.	S
<i>Amorpha canescens</i>	P	<i>Aster azureus</i>	S
<i>Amorpha fruticosa</i>		<i>Vernonia baldwinii</i>	P
Anacardiaceae		<i>Erigeron philadelphicus</i>	(♂)
<i>Rhus aromatica</i>		<i>Rudbeckia hirta</i>	
<i>Rhus copallina</i>	P	<i>Echinacea pallida</i>	
<i>Rhus glabra</i>		<i>Ratibida pinnata</i>	

have preferences for certain sorts of flowers. Such preferences doubtless occur among most polylectic bees and are responsible for the observation that at a given time different polylectic species often use different flowers in the same area. Such observations are very easily made with various species of *Trigona* and *Melipona* (see Michener, 1946).

Methods of Foraging: Methods of gathering pollen vary according to the flower being utilized as a food source. When working about over the masses of small flowers of *Rhus copallina*, the females can be rather easily seen to brush the anthers with the fore tarsi, to transfer the pollen to the middle legs, and thence to the scopa on the rear legs and probably to the hairs of the abdominal sterna. There is no regular timing of the movements, nor is there regular alternation of the movements; that is, sometimes pollen is trans-

ferred backward twice in succession on one side of the body before the same action occurs on the other side.

It seems that basically similar actions are used for collecting pollen on other flowers, but the modifications resulting from different flower structure are great. For example, to gather pollen from the flowers of *Plantago rugelii*, the bee alights on the long stamens, and as she hangs downward she clasps several of them together with the hind legs, then brushes pollen off of the anthers with the forelegs, transferring it backward to the scopa by the process already described. The bee flies from place to place on the flower mass; walking among the stamens looks to be impractical. It appears that pollen gathering must vary greatly in efficiency on different flowers.

Observations of pollen collecting bees in areas of mixed flowers showed that on any given trip a bee usually gathered pollen from a single kind of flower instead of going to various kinds and obtaining mixed pollen loads. Observations of marked bees going in and out of a single nest often showed that they were collecting from different flowers. For example, one might bring in loads of yellow pollen while another was bringing white. Moreover, a single bee might change the type of pollen it was gathering, so that after a yellow load, she might bring a white one.

Sometimes bees collecting pollen may suck nectar from another flower, then go on collecting pollen from the first. For example, a bee was seen collecting pollen of *Plantago*. She then flew to *Melilotus alba*, sucked some nectar, and returned to collecting pollen on *Plantago*. *Melilotus alba* is sometimes used as a pollen source, although perhaps not when *Plantago* pollen is also available.

Sometimes bees are seen to return to the nest with only a light dusting of pollen on the scopa. Presumably such bees were gathering nectar or feeding and in brushing among anthers, some pollen adhered to their hairs. What becomes of such pollen is quite unknown.

In late fall, after most of the flowers have disappeared, overwintering queens sometimes feed on honeydew. Details of this will be given in the section "Behavior of Queens."

Activity Around the Nests: Most of the activity of female bees around their nests has to do with coming and going of the bees. Bees leaving the nests often fly directly and promptly away from the nest entrance. Sometimes, especially in cool weather or in the early morning, bees come out of the hole very slowly, turning the

head jerkily from side to side, often lingering half exposed for some seconds, and may crawl as much as a centimeter from the hole before flying. In flight, the departing bee may dart away with very little "orientation flight" over the nesting area. This is particularly characteristic of departures occurring during the heat of summer days. On cooler days and in early morning hours, it is more common to see irregular zig zag or sometimes spiral "orientation flights" as bees leave. Such a flight requires up to 15 seconds, and during it the bee rises to a height of some four centimeters above the ground surface, flying about over an area of up to 30 cm. in diameter, although usually smaller, before making off. Figure 2 illustrates some flight patterns of bees leaving nests.

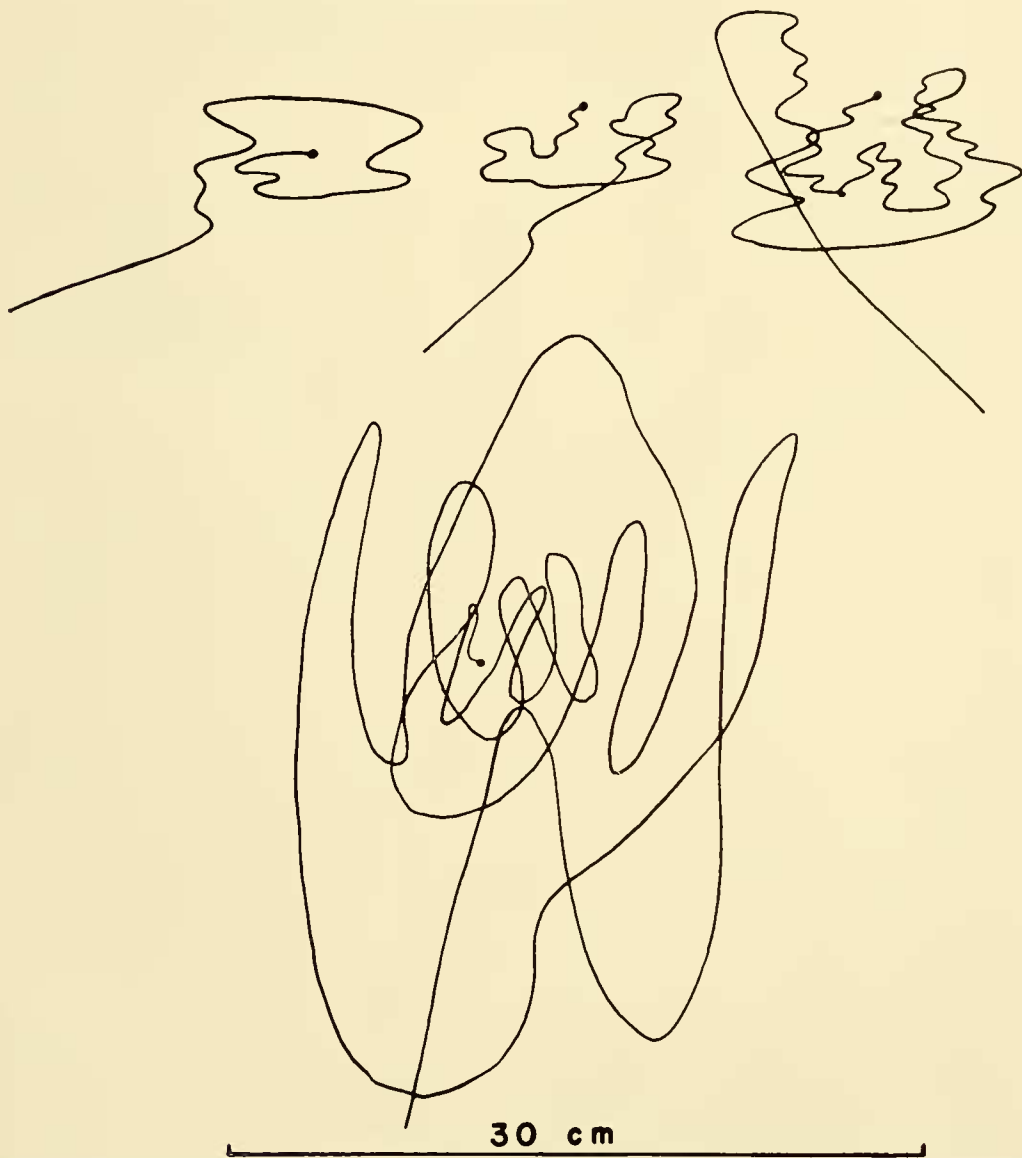


FIGURE 2. Flight patterns of females leaving nests. The lower one represents an unusually extensive "orientation flight."

The more elaborate and prolonged forms of departure mentioned in the preceding paragraph are characteristic, often in exaggerated form, of young adults. We noted this on several occasions, when activities of marked pollen collectors were being observed day after day. As unmarked bees began making trips from such a nest, they almost always made more elaborate departures than the presumably older, marked, foraging bees leaving the nest at the same time. A few days later the unmarked bees were seen collecting pollen and making the usual quick departures.

Bees accustomed to the nest usually fly almost directly to it, zig zagging only slightly in the last few centimeters of the approach to the nest. They alight almost at the threshold of the hole and quickly crawl in. Queens going into their nests in spring, and young females at other seasons, often seem to have difficulty finding their nests. They may alight on the ground near the nest, and after walking about, even starting to dig, they fly again, often repeating the performance for 15 or 30 minutes until they ultimately find the nest entrance. It seems apparent that such bees have little difficulty in getting within about half a meter of the nest, but the exact location of the nest seems often to be discovered by chance. Of course the number of such disoriented bees is greatly increased by any disturbance of the soil surface, such as trampling by cattle or persons, which may occur while bees are afield.

Occasionally disoriented bees enter the wrong nest, but usually soon leave again. The probability exists, however, that they may sometimes become incorporated into the populations of other nests as suggested by the results of the experiments on transferral of young workers from nest to nest, as described in the section on "Behavior of Workers."

Collections of disoriented or lost bees in locations where no surface disturbance could account for disorientation revealed not only young bees with unworn mandibles, as would be expected from the preceding paragraphs, but also some bees with much worn or very much worn mandibles. Presumably these are senile bees; the few dissected have all been workers. Like the unworn ones they give every impression of looking for their nests, examining every little hole, sometimes starting to dig, but soon walking or flying on. Such lost bees sometimes go away from the nesting area for half an hour or more, then return and resume their searching. We have marked such bees with paint and found them still searching the next day. We presume that some senile bees lose their ability to

return to their nests. In two cases which we observed, lost bees were individuals that had been previously marked and their activities observed in certain nests. In both cases the nests were seemingly normal, and exhibited normal activity, while the disoriented senile bees searched within a meter or two of their nests.

Duration of Trips and Periods Between Them: The data on this subject were obtained by means of bees marked for individual recognition. Most of the data were gathered from marked workers, but queens in the spring, when they are provisioning cells, make trips of similar duration and similar variability in duration. The in-

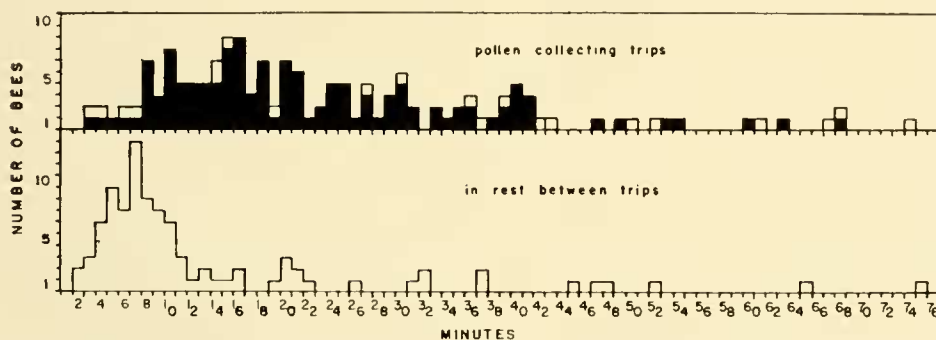


FIGURE 3. Histograms showing (above) durations in minutes of trips away from nests, black areas indicating that the bees returned to the nests with a pollen load on the scopa, and (below) durations of periods that bees spent in the nests between pollen-collecting trips.

formation on queens has therefore been lumped with that obtained by observing workers, and is presented in Figure 3.

Because pollen-collecting bees usually enter and leave their nests rapidly, it was found difficult to sit beside one or two nests and record every entry or departure. Sometimes bees would be missed altogether; more often they would be seen but their color markings could not be recorded with certainty. To slow down the bees entering the nests, we often put a straw or grass blade across the nest entrance. The resultant delay enabled us to record the color combinations of entering bees, but did not help with the departing individuals which would crawl from beneath the obstruction and immediately take wing. Therefore we have over one hundred records of the period from a time when a bee entered her nest until the next time that she entered her nest. These data support the picture indicated by Figure 3. In two cases the period from one entrance to the next was over 200 minutes.

We have records of trips from which bees returned with pollen loads on the legs ranging from 3 to 105 minutes in duration. As shown in Figure 3 the bulk of such trips take from 8 to 40 minutes,

with the maximum number of trips requiring about 16 minutes. The great variation in duration of trips may be due to variations in the ease with which pollen is obtained. There is some tendency for a series of successive trips by a single bee to be of about the same duration, as shown by this example (time given in minutes, P signifies return with pollen load): 13P, 24P, 13P, 15P; another example, 8P, 9P, 9P. However, durations of successive trips may vary strikingly, as shown by the following series: 36, 40P, 15P, 11P and 15P, 14P, 8P, 5P.

Successive periods spent in the nest between trips often vary considerably, as shown by the following five series (given in minutes): 4, 5, 5; 6, 2, ?, 6; 3, 2, 4, 9, 7; 8, 31, 9; 6, 7, 16, 37. As shown by Figure 3, the range of variation is far less than for trips afield. In the case of the last series shown above, the 37 minute stay in the nest was due to the bee spending a considerable time as a guard before leaving on the last trip.

These data in general show rapid trips and in theory a bee ought to be able to make many trips per day. As shown in Figure 1, however, outside activity of all sorts and pollen collecting trips particularly, diminish in the afternoons. The largest number of pollen collecting trips that we have ever seen a bee make in a day is seven. We often watched nests until activity seemed to have ceased for the day, and we are confident that more than seven trips per day would be unusual.

By no means all of the bees in a nest that are apparently able to collect pollen actually do so actively at any one time. This is shown in Table II, which shows the number of pollen collecting trips made by various workers during periods of three hours. As indicated by the zeros, a considerable number of workers made no trips whatever. Some of these were presumably young adults not yet ready to undertake foraging activities but others had been seen returning with pollen on previous days. It is also evident from Table II that many make only one or two trips during the time that others make five or six. The trips of the bees making few trips take no more time, on the average, than those made by bees making more trips. Rather, the bees making few trips seem to start late, stop early, or both, thus spending much more time in their nests.

In connection with the above paragraphs it should be mentioned that the data were collected from some of the most active nests and on days of great activity. The majority were less active, and nests like nest 1, Table II, which showed no activity in three hours, were common.

TABLE II.—Number of Pollen Loads Carried into Nests by Individual Bees During Periods of Three Hours Duration. Opposite "Number of Workers" is indicated the number of workers (marked for individual recognition) known to be present in the nest on the day when it was observed continuously for three hours. Opposite and below "Number of pollen loads" is indicated, for each worker, the number of loads that she carried into the nest. Data from different nests or different days are separated in lettered vertical columns. All data were gathered during the morning hours, *e. g.*, 8 a. m. to 11:00 a. m. or 9:00 a. m. to 12:00 a. m., during the months of June, July, or August.

Nest.....	a	b	c	d	d	e	f	f	g	h	i	j	k	l
Number of workers.....	8	8	7	7	7	7	6	6	6	5	5	5	4	4
Number of pollen loads for each worker.....	6	5	4	2	3	4	2	3	3	4	3	1	6	0
(Most active foragers above, least active below)	5	2	4	1	3	1	1	2	2	4	2	1	2	0
	3	1	2	1	1	1	1	0	2	0	1	0	1	0
	2	0	1	1	0	0	0	0	1	0	0	0	0	0
	1	0	1	0	0	0	0	0	0	0	0	0		
	1	0	0	0	0	0	0	0	0	0				
	0	0	0	0	0	0	0	0						
	0	0	0	0	0	0								
Total pollen loads.....	18	8	12	5	7	6	4	5	8	8	6	2	9	0

Variability in activity among nests is the rule rather than the exception. For example on July 3, 1952, three nests within 10 cm. of one another at Engle's Place were observed all day. In one, six different marked bees were seen at the entrance or going in and out, some of them busily carrying pollen. In another nest, two bees were seen, one of which made one trip afield. In the third nest, only a guard was seen, and she never left the nest. Such diversity is associated with varying nest populations resulting in part from variations in the number and activity of queens. In a population in which many colonies are dying throughout the year, one must expect to find many nests which seem inactive because of dwindling populations. However, we often also found relatively inactive colonies which later became active, presumably because of emergence of additional workers.

Probable Lack of Social Facilitation: Observers watching nests of *L. inconspicuum* (as well as other colonial halictines) are often impressed by the fact that there seems to be a tendency for several individuals to leave a nest or return to it in a short space of time. It sometimes happens that after watching a nest for many minutes and seeing no activity, an observer sees several bees leave within a period of five or ten minutes.

To determine whether there was social facilitation so that departure of one individual tended to be associated with departure of others, departures as well as arrivals during nineteen morning periods of good weather ranging in length from 60 to 190 minutes were tabulated. The observations were made at various nests and during all the summer months. The periods of observation were divided into ten minute units. There were 179 such units during which bees leaving the nests had been noted and 162 when bees entering nest had been recorded. During about 150 of the periods both arrivals and departures were recorded; during the remainder only departures or only arrivals were noted for one reason or another. The results of this study are shown in Table III. It can be seen that for both entering and departing bees, the frequencies of two or more per ten minute period exceed the frequencies expected from the Poisson distribution. The differences from the Poisson distributions are not statistically significant, however, for departures and are scarcely so ($.02 < X^2 < .05$) for arrivals. The consistency of the differences for the two sorts of data (arrivals and departures) suggests that they may not be mere sampling errors. They might result from external factors (a cloud over the sun or the presence

TABLE III.—Numbers of Females Entering or Leaving Nests During Ten Minute Periods. Most of those entering carried pollen loads on their legs.

Bees per ten minute period	Observed and expected frequencies			
	Entering		Departing	
	Observed	Expected	Observed	Expected
0.....	60	59.60	70	72.78
1.....	54	59.60	64	65.50
2.....	31	29.79	30	29.48
3.....	12	9.93	9	8.84
4.....	3	2.48	4	1.99
5.....	2	.50	1	.36
6.....			1	.05
Totals.....	162	179

of the observer) holding up departure or return of foragers for a time until several are ready to leave or return at about the same time. Alternatively, guards may sometimes retard departures until several bees are ready to go.

Since the study reported in Table III seemed inconclusive, and since it seemed desirable to relate arrivals at a nest with the departures immediately following them,¹ another study was made, again based on morning observations made during good weather. Because the units of time used were five instead of ten minutes, in length, it seemed reasonable to include briefer periods of observation in the study; twenty-five periods ranging from 40 to 190 minutes in duration were used. Both arrivals and departures were recorded during these periods. The average number of departures for five minutes was determined for each period of observation (Table IV, column 2). If departures were associated with arrivals, then the average number of departures per five minutes following an arrival should exceed the general average number per five minute period. Column 3, Table IV, shows the average number of de-

1. Arrivals of successful forages are related to departures of other foragers in many social insects, such as *Apis*, *Trigona*, *Melipona*, *Bombus*, *Polistes*, *Vespula*, and many ants.

TABLE IV.—Average Number of Females Leaving Nests in Consecutive Five-minute Periods (Column 2) and in Five-minute Periods Starting with the Return of a Bee.

(1) Observational period	(2) Mean number of departures per five minutes	(3) Mean number of departures in five minutes following arrivals	(4) Duration of observations (minutes)
1	.15	0	100
2	.17	0	90
3	.20	0	50
4	.25	0	40
5	.27	.33	75
6	.28	.25	70
7	.29	.67	70
8	.30	.09	185
9	.31	.70	145
10	.31	.83	145
11	.36	.40	140
12	.36	.35	100
13	.36	.22	100
14	.36	.67	95
15	.39	.58	190
16	.44	.80	45
17	.49	.52	185
18	.55	1.00	110
19	.58	.50	155
20	.60	.86	50
21	.76	.33	75
22	.78	.67	45
23	.85	1.23	65
24	.88	2.00	40
25	1.13	1.00	75
Mean	.46	.56	

partures in five minute periods, each of which starts at the moment of arrival of a bee (almost always a pollen-laden forager).

Examination of Table IV, in which the observational periods are arranged in order of increasing mean departure rate, shows that when there is little activity, the few departures seem to have little relation to the arrivals. At low departure rates, assuming no relation between an arrival and the ensuing departure, it is not surprising that the departures commonly fall in the long intervals

between arrivals. When there is more activity in nests, the number of departures per five minutes following arrivals clearly exceeds, in most instances, the mean number of departures per five minutes. At first thought this would seem to indicate some sort of social facilitation in which the return of a forager stimulates the departure of others, acting either through the guards or directly upon other foragers. This is apparently not true, however, for Figure 3 shows that some 28 percent of the periods between trips by a given forager are five minutes or less. Excluding first trips for the day, this percentage of the departures is in reality associated with arrivals for purposes of the five-minute units used in this study. Therefore it is not surprising that the excess of the mean of Column 3, Table IV over that of Column 2 is 22 percent. In any event this excess clearly does not show an influence of returning foragers on different departing ones.

Lack of social facilitation of foraging trips is hardly surprising in a primitively social form such as *L. inconspicuum* with the nests branched and cells dispersed.

Length of Flights: In early spring when flowers are scarce, one sometimes finds nests being provisioned a considerable distance from any flowers. We have seen such nests as much as 50 meters from the nearest flowers (*Prunus*) that we could find. Presumably the bees fly at least that far.

During the rest of the active season flowers are so generally available that it was never far to them from the nesting sites that we found. We experimented with carrying marked pollen collecting bees away from their nest and releasing them. We assumed that if they found their way back quickly, they were probably familiar with the landmarks at the place where they were liberated. Bees returned promptly from points 75 meters distant from their nest. Unfortunately the experiment was not continued to the point where some of the bees were lost, but it does indicate that in spite of their minute size, these bees fly moderate distances.

NESTS

Distribution of Nests: Nests have been found in the soil of a wide variety of sunny or partly sunny locations. Undoubtedly many of the nests are isolated. Because of their inconspicuousness, solitary nests are difficult to find. We came upon them occasionally, however, in overgrazed pastures, parkings or partly bare areas on the University campus, along an abandoned road, etc. Those that

we studied or excavated seemed quite comparable to nests in aggregations.

It was convenient for us to make our studies in places where we could find numerous nests in the same vicinity. Fortunately several such locations were found, after much and often fruitless searching, in the vicinity of Lawrence, Kansas. The accounts of these places below give some idea of habitats in which *Lasioglossum inconspicuum* nests. The locations are sufficiently variable that we have never been able to learn how to recognize a nesting area from a distance. This is because of the great amount of ground seemingly similar to that of the nesting aggregations, and yet without nests or with only widely scattered, isolated ones.

Even in the aggregations, the nests were not closely placed. In late spring, when the number of nests is at its maximum, there were occasionally found places having perhaps ten nests in an area of one fourth square meter. These were exceptional local concentrations within larger aggregations. By midsummer or fall most of the nests established in spring are dead, and often there was only about one nest per square meter in the aggregations. The aggregations are loose and usually lack definite margins because with careful searching scattered nests can often be found in the surrounding areas.

The nine aggregations from which we obtained nearly all of our data on *Lasioglossum inconspicuum* are briefly described as follows:

1. *Potter's Lake*. This is on the campus of the University of Kansas. The nests were found along a slightly sloping path which received considerable use. Although a few isolated nests were found from time to time elsewhere along this path, most of them were in an area about 10 meters long and 2 meters wide. Scattered plants of bluegrass (*Poa*) and plantain (*Plantago rugelii*) grew in and especially along the sides of the path. The nests were often found among these plants as well as in areas of bare soil. Large trees (elm and hackberry) shaded the path except during four or five midday hours. In one area where new nests were established each spring before leaves grew on the trees, shade continued nearly all day when the trees were fully leaved. In this shady place nests died out in early summer. The mortality of nests elsewhere was so high, however, that one could not be certain of the effect of shading on survival of the nests. The soil was hard and rather crumbly when dry, with considerable amounts of clay. The surface was often dusty due to foot travel along the path. It

was in a low area, however, and remained moist longer than soil of the hill tops.

Among nests of *L. inconspicuus* at Potter's Lake were numerous nests of *Andrena erythronii* Robertson (area II of Michener and Rettenmeyer, 1956) and during the earlier years of observation, *Calliopsis andreniformis* Smith. Other bees nested in the area only occasionally.

2. *Cooper's Place*. There were two sites grouped together under this name in a little used pasture about nine miles southeast of Lawrence. They were on nearly flat but well drained ground, and were in small areas of short sparse grass where the soil surface was exposed to the sun. Each of the areas was about five meters across. There were no nearby trees or large bushes to provide shade. The main vegetation outside the immediate areas where the nests were found consisted of *Symphoricarpus orbiculatus* and *Rhus copallina*. The nests were in surface soil of Dennis Fine Sandy Loam, developed on sandstone.

In one of the two areas in the pasture, enormous numbers of nests of *Lasioglossum (Chloralictus) rohweri* (Ellis) occurred in 1951, but not in subsequent years. A few nests of *Augochlorella aurata* (Smith) and *A. striata* (Provancher) also were found in the same area.

In the spring of 1957 the pasture was plowed and sown, destroying it for the time being as a nesting place.

3. *Engle's Place*. The nesting area called by this name consisted of some nearly bare areas sparsely inhabited by *L. inconspicuus* in an overgrazed pasture about eight miles southeast of Lawrence. The ground was gently sloping, well drained, and high enough to be quite dry. The vegetation was sparse; aside from scattered trees of hedge apple (*Maclura pomifera*) which did not shade the nesting areas, the principal vegetation was weeds such as *Vernonia baldwini*. The soil was like that of Cooper's Place.

In the spring of 1957 the area was plowed, destroying it for use by *L. inconspicuus* as long as cultivation is continued.

4. *Intersection* (Figure 40). This area was on a dry, rocky hill about nine miles southeast of Lawrence. The ground in the nesting area was flat. It was protected from grazing and had never been cultivated, but had been much disturbed because it was on the former site of a schoolhouse. Perhaps because of its rockiness, vegetation was not everywhere dense; there was an area about

six meters square largely occupied by sparse vegetation so that the soil surface was largely exposed. There was no shading by bushes or trees. In this area the principal plants were tall grasses and *Verbena stricta*. Outside of the nesting area the same plants, together with *Rhus copallina* and others, formed dense masses which made the ground there unsuitable for nesting of *L. inconspicuum*. Because of removal of the surface soil at some time in the past, the nests were in subsoil of Dennis Fine Sandy Loam, developed on sandstone.

A few nests of *Halictus confusus* Smith were found in the same area.

5. *State Property*. The area called by this name was about two miles southwest of Lawrence, on a gentle slope. Although not cultivated for many years, if ever, native vegetation was entirely gone and replaced by weeds. Hedge apples (*Maclura pomifera*) were nearby trees, but did not shade the nesting area. The nesting area itself was sparsely covered with grass, unlike much of the adjacent ground which was densely weedy or grassy. The soil was Newtonia Silty Clay Loam developed on Oread Limestone. The nests occurred in a space of about four square meters and were associated with burrows of *Augochlorella striata* (Provancher) and *A. aurata* (Smith).

After 1955 no nests of *Lasioglossum* were found in this area, probably because the grass became dense in the nesting place.

6. *Sycamore Slope* (Figure 38). This area, on the University of Kansas Natural History Reservation, was in ground cultivated at one time, but since 1946 it has been sown with native prairie grasses and left strictly alone. The nests were on the sides and summits of some small bare ridges resulting from erosion. The nests were found in an area about three meters on a side. There was no shade. Nests of *Augochlorella aurata* (Smith) and *striata* (Provancher) were associated with those of *Lasioglossum*. Another area in which we found some nests was along the side of the road near the main sycamore slope area. Both of these places are upland areas of severely eroded Pawnee Silty Clay Loam developed on glacial drift.

7. *Prairie Road* (Figure 39). This was on another part of the University of Kansas Natural History Reservation. An abandoned road (merely a pair of wheel tracks) crosses few acres of upland prairie that has never been cultivated. In one section of this road, about seven meters long, nests were found in considerable numbers

both in the exposed soil and along the edges of the tracks where they were largely shaded by overhanging prairie plants. Elsewhere along the same road across similar soil, there were only occasional isolated nests. Vegetation consisted of typical prairie plants with some intrusion of *Rhus copallina*. The soil at this location was a Newtonia-like Silty Loam developed on limestone.

8. *Petefish's Place*. The nests at this location were in a level area about three meters square of mixed sand and clay along a stream five miles southwest of Lawrence. The location was so low that it must have been flooded most years; flooding was shown by the bent grass and drift wood at the time of our work in this area. The surface was bare except for scattered clumps of grass and of sweet clover, *Melilotus alba*. The area was exposed to the sun most of the day but was shaded in the later parts of the afternoons by elms, hackberries, and other trees. The soil was a sandy loam, quite loose and obviously more sandy than at any other location where this species was studied.

9. *County Line*: This was an overgrazed upland pasture along the Douglas County-Franklin County line south of Lawrence. There was sparse grass and abundant weeds, such as especially *Vernonia baldwini*. The nests were widely scattered in small bare areas in the pasture. There was no shade except that afforded by the grass and weeds.

Common Features of Nesting Areas: From the descriptions of nesting areas given above it is possible to extract some common features which are presumably necessary for nesting by this species. The soil surface is flat or gently sloping in all cases. It must be exposed; no nests were found where the soil was densely covered by vegetation (as on undisturbed portions of prairies or in densely weedy areas) or by fallen leaves (as on the forest floor). The nesting site is typically exposed to the sun all or most of the day. Nests started in the spring under deciduous trees disappeared after the foliage cast its shade. The soil was in all cases loam, usually surface soil but sometimes subsoil. The soil may be derived from sandstone, limestone, or glacial drift. Nesting may occur in prairie soil disturbed only by removal of vegetation or in areas that were once plowed and have been severely eroded or even in streamside sandy loam deposits. In spite of all this variation in soils used, the material is always compact and often hard; nests never occur in loose sandy soils. Nesting may occur in stony situations where nests must curve around the rocks or penetrate them if not too

hard. Nests may be found on hilltops, slopes, or in stream valleys. As explained in the section on "Survival of Nests" below, we think that lack of moisture in soil sometimes results in death of colonies of the bees.

Because of destruction of natural forests and prairies, heavy grazing, and sheet erosion, very numerous areas provide the requirements for nestling noted above. Some possible reasons for development of aggregations will be discussed in the section on "Distribution of Nests."

Differences in Activities Among Nesting Areas: Differences in activities among the various nesting areas were often noted. Thus in late May and early June, 1952, we noted that some nests at Cooper's Place were still being provisioned by the founding queens, that there were no smooth areas around the nest entrances nor were there guards, and that most of the nests were closed and unrecognizable. At the same time at Potter's Lake many of the nests had already produced workers which guarded the well-formed entrances and made smooth areas around them; queens were probably rarely seen at the surface of the ground. Not until June 5 did these features appear in the Cooper's Place population.

Later we noted that guards in the nests at Cooper's Place appeared to be timid and disappeared into their nests at the slightest disturbance; only rarely would they turn and block the entrance with the abdomen and then only well down below the surface of the soil. At Potter's Lake the guards were much less easily disturbed, and when disturbed they readily turned and blocked the entrance with the abdomen, doing so close enough to the surface that they could easily be marked with paint for individual recognition while in this position.

On July 5, 1952, we noted that colonies at Potter's Lake and Cooper's Place had been inactive for several days, possibly because of prolonged dry, hot weather (reaching 39° to 41° C. daily in shade), but colonies at Petefish's Place remained active, possibly because of the low, cool location near a stream.

In examining nests in different locations, we found that there is a strong tendency for nests in any one location to be similar in depth and form. This is probably because of differences in soil (including soil moisture) in different places. For example, in midsummer, nests at Cooper's Place tended to be deep (usually over 65 cm.), and little branched except at the lower levels where there were cells. At the same season nests from Potter's Lake were rarely over

60 cm. in depth, usually shallower, and often rather broadly branched even at the upper levels.

These examples illustrate the danger of generalizing from nests observed in only one location or for only a brief period.

Survival of Nesting Aggregations: As already indicated, several of the areas described above were occupied by nests of *L. inconspicuum* over a period of several years. The site at Potter's Lake had nests in it every year of our study. Sometimes in late summer there were only one or two nests known to us in the area, but each spring a new lot of overwintered queens established nests there. At Cooper's Place, one of the areas had nests for only two years but the other was occupied each year until it was plowed in 1957. Sometimes in late summer or fall not one nest could be found in the area, but in spring it was always reoccupied. Similar observations were made at other areas of aggregation. There was consistently a relatively enormous mortality of nests during each season of activity.

Sometimes, as at the roadside aggregation at Sycamore Slope, although numerous nests were seen in April and May, not one could be found by mid-June. More often a few survived for the entire year. During dry summers we sometimes got the impression that soil humidity was an important factor in nest survival. At the Intersection site, which often became very dry, excavation of nests in August showed that the only ones surviving were those that actually penetrated relatively moist sandstone rock. At Potter's Lake also, one August when but few nests survived, we found that those which we dug penetrated chunks of moist sandstone scattered deep in the soil. These observations, combined with the fact that nests are dug deeper and deeper during the summer at the same time that the soil is becoming dryer, led to our surmise that lack of soil humidity was an important factor in mortality of nests. During the drouth years of 1953 to 56, some of the nest aggregations became entirely extinct, not even being replenished in spring. This occurred at the Intersection, an obviously dry hilltop; at Petefish's Place where the soil became very dry in appearance, probably because of its sandiness, in spite of its low lying location, and probably at Engle's Place. We only have knowledge of Petefish's Place being occupied one summer; it is the most abnormal of the sites found.

During years of adequate and high rainfall many nests also die. We were not, in fact, able to study any nest aggregation for any

season without being impressed at the high rate of mortality for which we have no satisfactory explanation.

The question of the source of the overwintered queens which establish nests in the spring is interesting. There is a surprising number of such bees considering the late spring and summer mortality of nests. Presumably they come from the nests that did survive the summer in the areas of aggregation as well as from the isolated nests. The latter are doubtless far more numerous than out data suggest, for the minute holes in the soil are difficult to find. Among nests excavated in the fall and early winter, the average production of young queens was between six and seven, with a maximum of 18 observed on one occasion. Most of these bees disperse in the spring from their parental nests and establish new ones.

Survival of Nests: Numerous individual nests were marked with numbered nails pushed into the soil a few centimeters from each nest. Each group so marked and used for the present aspect of the study consisted of nests in a single aggregation. The number of marked nests in each group is indicated in Figure 4. The nests were re-examined at daily, weekly, or occasionally less frequent intervals. As will be explained later, nests are often closed temporarily. Colonies were considered as dead only when repeated visits showed a nest to be permanently closed. Excavation of a considerable sample of such nests showed no surviving bees of any

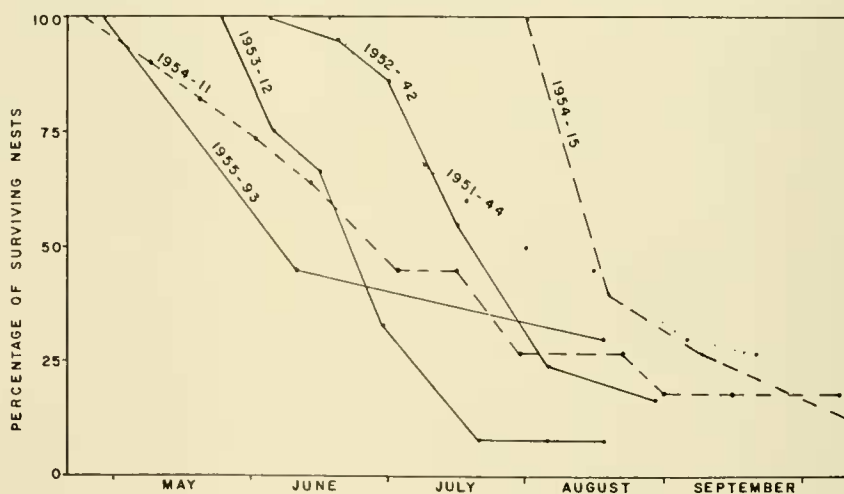


FIGURE 4. Survivorship curves for colonies in six aggregations. A colony was considered dead when its nest became permanently closed. The number of nests in each group is indicated, after the year, along each curve. Each group consisted of marked nests in a single aggregation.

age. Survivorship curves for each six groups of marked nests are shown in Figure 4.

It can be seen that in each group, nests succumbed for a time in such numbers that complete extermination before the end of summer seemed likely. As indicated above, this sometimes happens as aggregations of nests do sometimes become extinct. However, each of the curves shown in Figure 4 flattens out as the season progresses, showing that some nests survived through the summer (or at least until the end of the observations) in each case. Presumably this indicates that a relatively few nests, fortunate in location or in some other attribute, have a good chance of survival while the others die. This means that once a nest survives for a certain time, it has a good chance for longer existence.

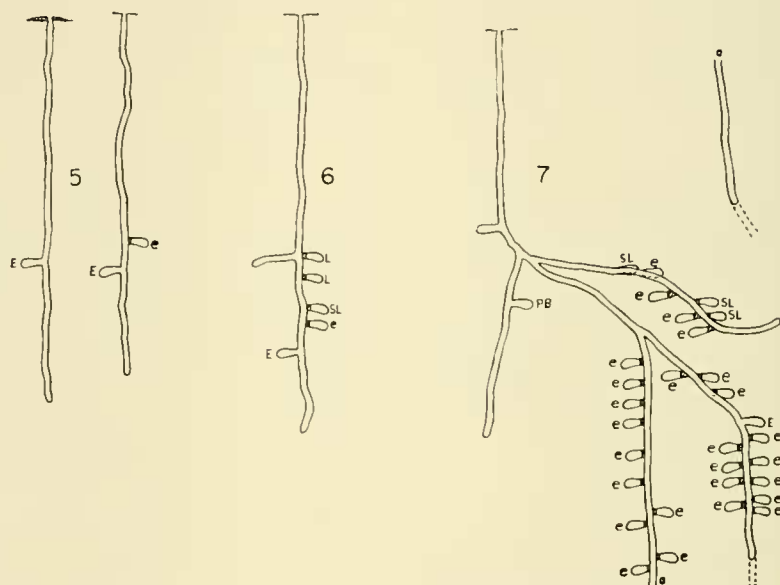
The group studied in 1953 reached a lower level earlier in the season than any of the others. It was at the Intersection, which as already explained was a dry location from which bees ultimately disappeared completely. The groups for 1951, 1952, and the first for 1954 (marked in April) were all at Potter's Lake while that marked in July, 1954 and that marked in 1955 were at Engle's Place.

For the great majority of nests, death of the population was not due to any of the obvious natural enemies (mutillids, *Paralictus*, mold attacking pollen masses). Probably death of the queen and failure to replace her, followed by death of the short-lived workers, was the common cause of extinction.

Nest Structure: The nests consist of burrows which extend essentially straight downward into the soil, but often meander considerably (Figures 5 to 16). In soil full of stones, there are often long horizontal sections following the surfaces of the stones until they reach places where they can go downward. Sometimes burrows, after passing through the soil for some distance, enter sandstone and perhaps other similarly soft rocks; as already suggested such nests sometimes survive better, possibly because of moisture in the rock, than their neighbors entirely in soil. The burrows range from 1.8 to 2.5 mm. in diameter, rarely reaching 3 mm. in diameter in certain parts of the nest. At the surface of the ground the burrows are narrowed to 1.3 to 1.5 mm. in diameter.

Nests made by single queens in the spring have no specialized structure at the surface and the minute holes are difficult to find. Holes occupied by more than one queen in the spring, and those occupied by queens and workers in summer, are ordinarily surrounded by a depressed smooth, shining area (Figure 41) which

appears to be thinly covered by a layer of material of perhaps salivary origin. These depressed areas are 3 to 4 mm. in diameter and the surface is usually horizontal. When the soil is dry they may be poorly kept and may even disappear due to pulverization of the soil but after a rain each active nest will again be provided with such an area. It is only when quite dry that the salivary layer covering the smooth area can be easily detected, for then it pulls away from the soil in places and therefore has a whitish appearance. Rarely in Kansas, we have observed such areas sloping inward, form-



FIGURES 5 to 7. Diagrams of nests. For these figures as well as Figures 8 to 16, several abbreviations and symbols are used. Cells indicated by broken lines are earth-filled. There were often more of these than indicated; and such cells are often omitted even though some were present, for they are hard to recognize unless very freshly filled with earth. The following letter symbols are used in connection with cells: e, egg; E, empty; EF, empty except for larval feces; L, larva of moderate size; LL, large larva and prepupa; M, cell contents destroyed by mold (fungus); P, pupa (all females unless marked male); PB, pollen ball (but no egg or larva); SL, small larva. When diagrams have been broken to conserve space, connecting points are indicated by the same letters.

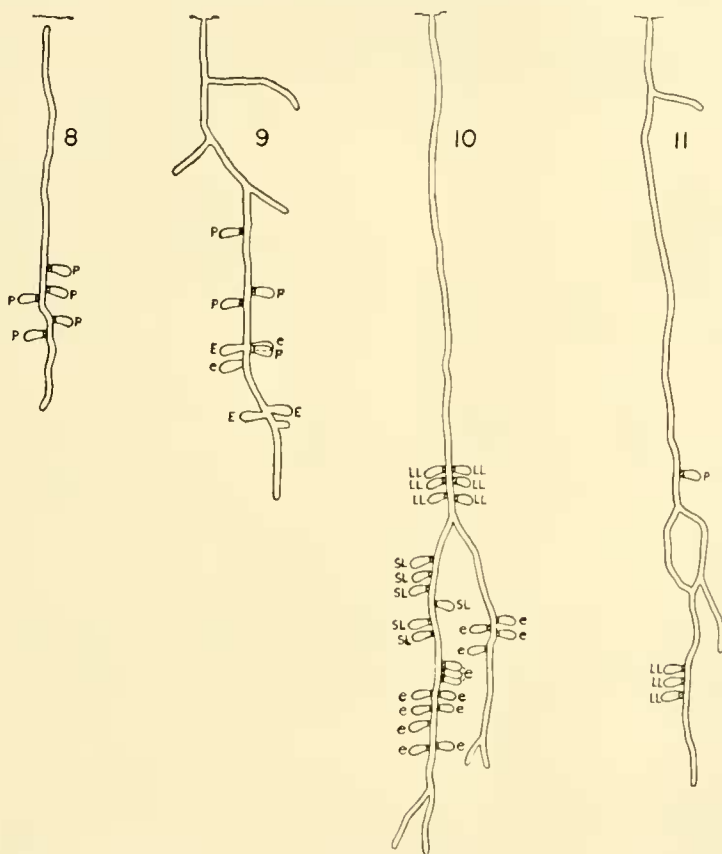
FIGURE 5. Two young queen nests opened on April 27. The one at the left has a fresh tumulus and a single empty cell. Each nest was occupied by a single queen.

FIGURE 6. A queen nest opened on May 6 showing sequence of the brood from oldest above to youngest below. The nest was occupied by a single queen.

FIGURE 7. An old nest opened on April 24 and found to be occupied by a group of four queens which were reusing the burrows of the previous season. Earthfilled burrows extending to deeper levels are indicated by broken lines.

ing small funnels around the entrance holes. One of us (C. D. M.) noted the entrances regularly funnel shaped, sometimes steeply so, at nests of this species in the garden of Mr. P. H. Timberlake at Riverside, California, where *L. inconspicuum* has been introduced from the eastern or central United States. Probably the form is in some way related to the texture of the soil.

When bees are digging, the excavated earth is pushed up to form a tumulus which spreads irregularly around the entrance and reaches diameters of 12 to 18 mm. The material of the tumulus is granular



FIGURES 8 to 11. Diagrams of nests. For symbols see explanation of Figures 5 to 7.

FIGURE 8. Closed queen nest opened for study on May 28. The nest was occupied by a single queen.

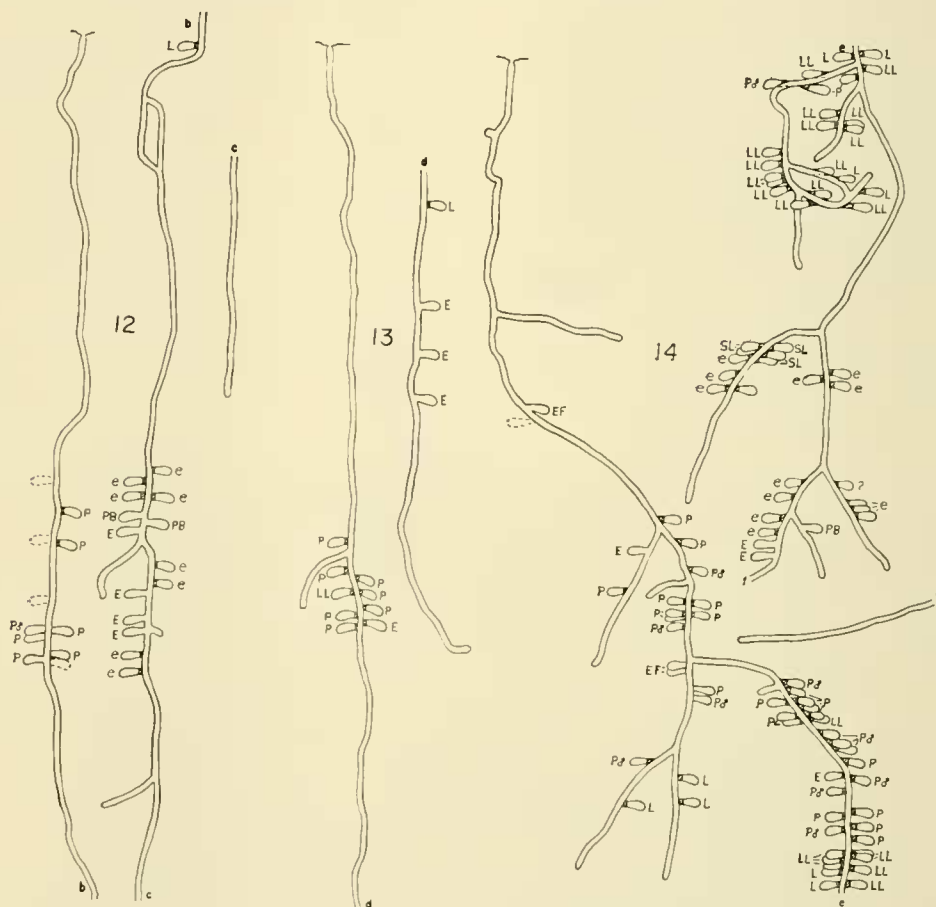
FIGURE 9. Nest opened on June 3. It was occupied by a single queen and two adult workers. Excavation beyond that of a queen nest is shown by the cells containing eggs, by the lower empty cells, and by the partially excavated cell lower than any completed cell.

FIGURE 10. Nest opened on July 16. It contained a queen, two workers, and one bee which escaped.

FIGURE 11. Nest opened on July 16. It contained only one queen and one worker. Obviously the queen had laid no eggs recently.

but often tends to cling together; the bees find their way through it in irregular passages, there is not a uniform passageway through it as is found in some species. The tumulus may cover the smooth area completely. Tumuli, however, are ephemeral structures which wash away in rains or are blown away by winds, leaving the entrances open and surrounded by obvious smooth areas.

We have not noted evidence of burrows being lined with dirt from deep in the nest, as is so often the case among other halictine bees [e. g., *Augochloropsis diversipennis* (Lepeletier), see Michener and Lange, 1959; and *Lasioglossum malachurum* (Kirby), Bonelli, 1948]. The burrows are round in cross-section, not especially smooth walled. Queen nests, established in the spring by single queens, range from

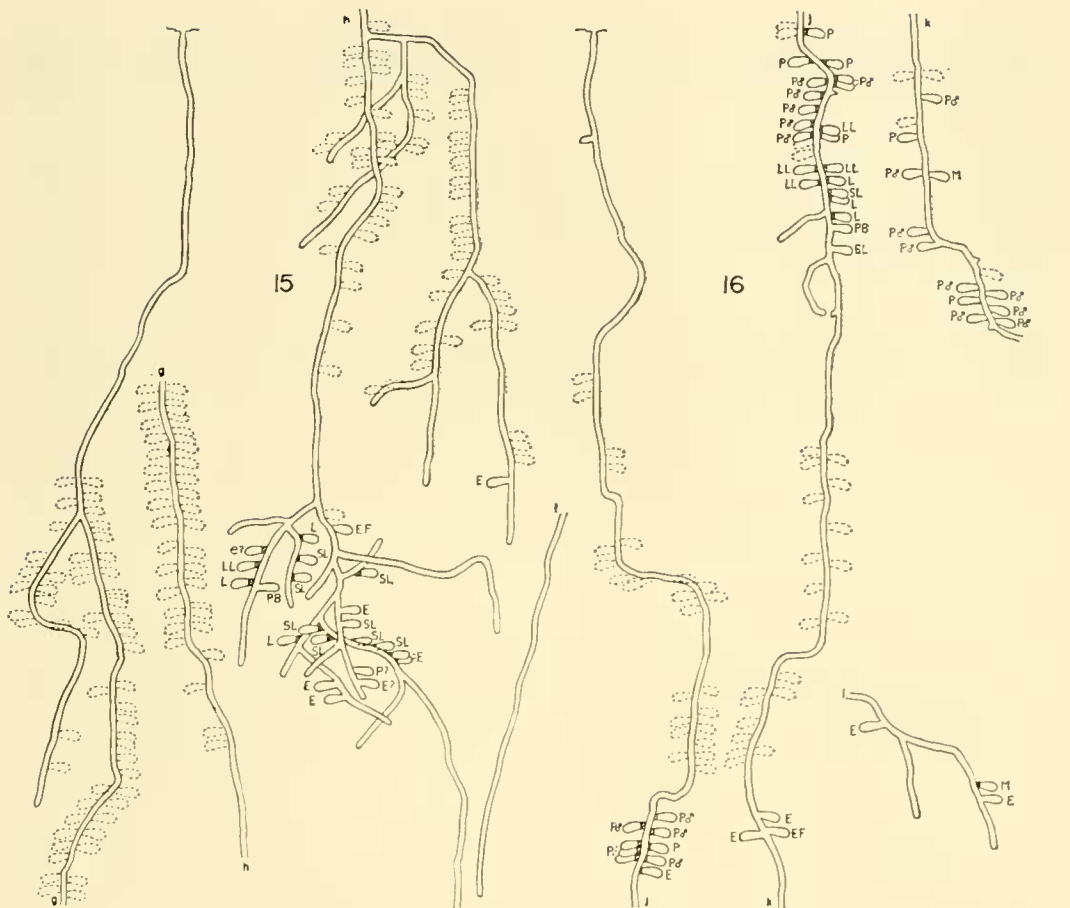


FIGURES 12 to 14. Diagrams of nests. For symbols see explanation of Figures 5 to 7.

FIGURE 12. Nest opened on July 1. It contained one old queen, five worn workers, and eleven unworn females almost all of which were certainly workers.

FIGURE 13. Nest opened on July 2. It contained one queen, five worn workers, and three unworn females that almost certainly were workers.

FIGURE 14. Nest opened on June 26. It contained one little worn queen, eight worn workers, and two unworn females that almost certainly were workers.



FIGURES 15 to 16. Diagrams of nests. For symbols see explanation of Figures 5 to 7.

FIGURE 15. Nest opened on August 4. It contained two queens, twenty workers, and two females of doubtful caste.

FIGURE 16. Nest opened on September 6. It contained one probable worn queen, eight worn workers, and two young females that might well have been overwintering queens.

9.5 to 24 cm. deep and the burrows are little branched (Figures 5, 6, 8, and 9). Nests occupied by two or more queens, usually or always using the burrows of the previous year in which the queens presumably hibernated, are often much deeper, and more fully branched (Figure 7); the deepest that we excavated was 55 cm. deep, and abandoned burrows filled with earth extended even deeper. Lower parts of such reused nests are always partially filled with soil in spring.

With production of workers the nests are extended deeper into the soil, and as shown in Figure 17 and Table V, maximum depths, on the average, are attained late in the summer. It is obvious that burrows are deepened during the summer. It is possible, however, there is differential survival of colonies that have made deeper nests, for as the soil dries during the summer, it may happen that only

deep nests reach levels where the soil is damp enough. If this is true, selection would probably favor colonies using nests of the previous year established by more than one queen. The enormous mortality of colonies noted in a preceding section was so far as known mostly in nests started by single queens. Colonies started each spring by several queens may occupy the same burrows for several years in succession and perhaps deepen the burrows somewhat each year. The lower parts become filled with dirt (often loose) during spring and early summer, but this may be cleaned out or new branches made during the summer. The deepest burrow

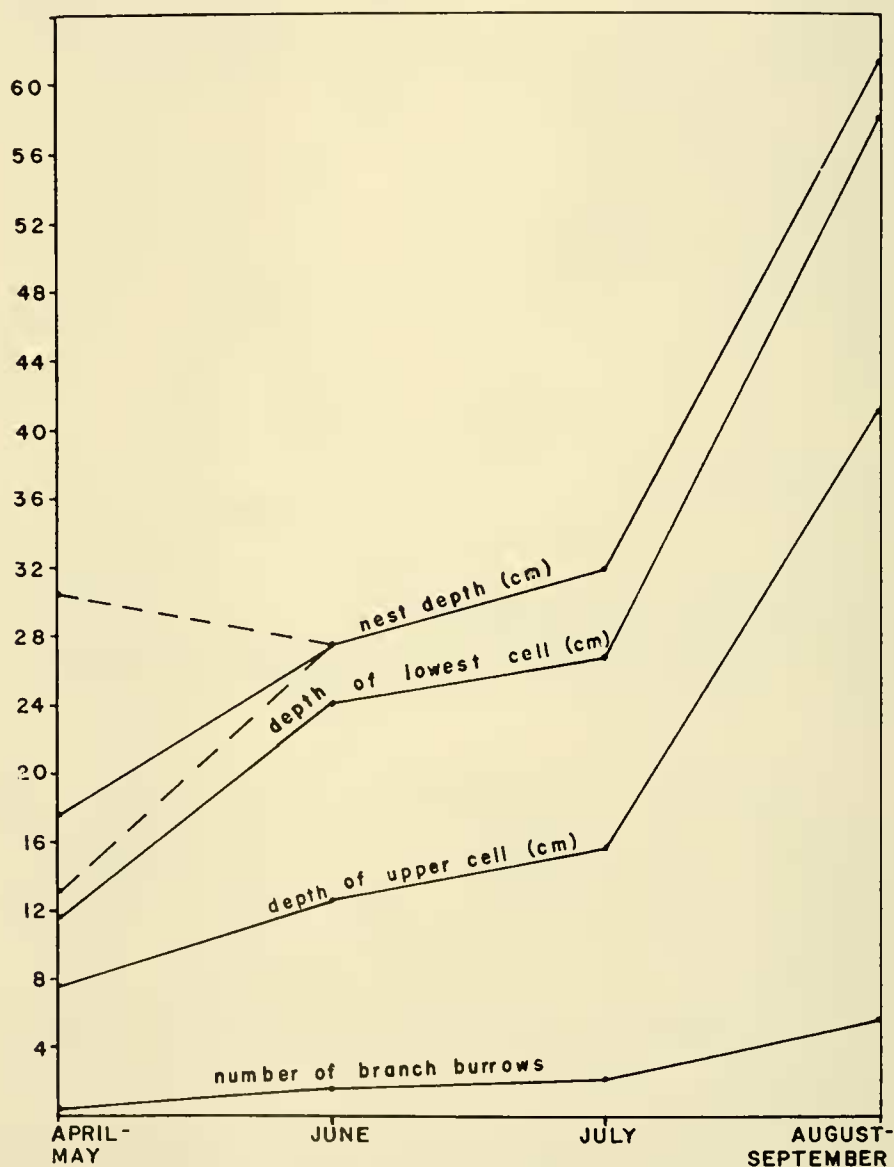


FIGURE 17. Graph showing mean nest depth, cell depths, and mean number of branch burrows. For April-May, broken lines also show depths of newly established nests and of old nests of the previous year that are being re-used. Other statistics concerning these matters appear in Table V.

found (in August) was 93 cm. deep, much branched after the manner of Figure 14. The shallowest, late summer or fall, burrow was only 14 cm. deep.

As shown in Figure 17 and Table V, the number of branch burrows is much greater in the large nests late in the season than in the small queen nests. Nonetheless the number of branches is not as well correlated with burrow depth as might be supposed. The correlation coefficient (r) of nest depth with number of branch burrows ranges from .45 to .50 during the summer months. Figure 14 shows a nest with about the maximum number of branch burrows, while Figures 13 and 16 show rather deep nests with few branches.

Of course the level of occupied cells descends with the deepening of the burrows (Figure 17 and Table V). In the queen nests in the spring the uppermost cell is quite regularly about 8 cm. below the

TABLE V.—Nest Depths (in centimeters) and Number of Branches. For total depths, statistics on new nests and on nests of the previous year are segregated in April and May. Later in the season it becomes impossible to distinguish new from old nests. n = number of nests examined; \bar{x} = mean; SE = standard error of mean.

	Nest depth				Depth of upper cell			
	n	\bar{x}	SE	range	n	\bar{x}	SE	range
April-May	46	17.54	1.539	9.5-55	47	7.74	.182	3.5-11
new	35	13.50	.452	9.5-24				
old	11	30.41	4.540	17-55				
June	31	27.56	1.960	10-52	30	12.50	.951	6.5-30
July	24	32.06	2.170	18-67	23	15.50	.951	9-27
August-September	26	61.23	4.656	14-93	21	41.02	4.515	7-63

	Depth of lower cell				Number of branches			
	n	\bar{x}	SE	range	n	\bar{x}	SE	range
April-May	27	11.72	.455	7-18	29	.48	.162	0-3
June	30	24.20	1.790	9-48	30	1.60	.568	0-11
July	22	26.82	2.188	13-55	24	2.21	.528	0-12
August-September	21	57.95	4.65	9-84	24	5.75	1.029	0-16

surface of the soil, although depths ranging from 3.5 to 11 cm. have been recorded. After workers mature and the burrows are deepened, new cells are constructed at deeper and deeper levels and at increasingly variable levels, as shown in Table V. Cells from which bees have emerged are filled with dirt, usually very soon after emergence, so that the number of used cells that have not been filled with earth in any one nest is always very small except occasionally when the adult population is for some reason much reduced.

The cells themselves are subhorizontal, sloping downward slightly to their posterior ends, bilaterally symmetrical, the lower surface being flatter than the others, very smooth on the inner surfaces which are lined with a thin coating of waxlike material (Figure 42). Measurements of cells range from 5 to 6.6 mm. in length and from 2.8 to 3.2 mm. in diameter. The variation in length is partly due to variation in the exceedingly short lateral burrows connecting cells to the main burrows. The laterals may be said to be so short as to be absent. Ordinarily after an egg is laid in a cell, it is closed by means of a plug of loose, friable soil. Sometimes when plaster of Paris is poured into a nest, it enters a few of the cells. We do not know if such cells were really open; perhaps the plaster merely pushed aside the delicate plugs. It is clear that plugs are normally present; it is also clear that plugs are absent or destroyed with equal frequency in cells of all ages, including those containing pupae. It is therefore most unlikely that there is any progressive feeding of larvae, since if that were the case one would expect to find plugs more frequently absent in cells containing larvae of certain ages. Occasionally a nest was found in which plaster entered nearly every cell. It should be remembered that in *L. malachurum* (Kirby) and other species in Europe some authors have insisted that the cells are open while others have found them closed. Perhaps there is variability in the strength of the plugs or even in their presence. Sakagami and Michener (in press) have discussed the various statements in the literature concerning this matter. As shown in the figures, the cells are often grouped more or less close together, but do not form distinct clusters as in some other halictine bees. (See discussion of halictine architecture by Sakagami and Michener, in press).

The numbers of cells in queen nests that had probably reached the age where no additional cells would be made until emergence of workers are shown in Figure 18. It is evident that nests made by a single queen usually contain about five cells, although there is

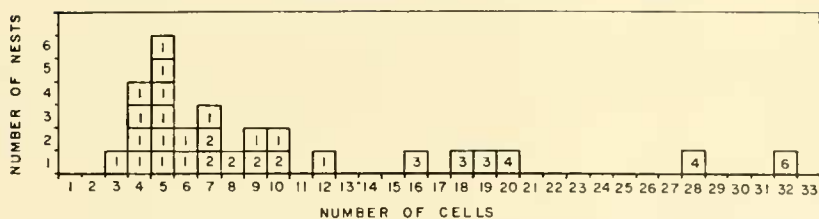


FIGURE 18. Histogram showing numbers of cells in queen nests. Queen nests containing only eggs and young larvae, or which for any other reason seemed to be still growing, were excluded from consideration. Exceptions are nests containing 28 and 32 cells which were included because of the large numbers of cells (and queens) even though they might have produced even more cells. The numbers in the squares indicate the number of queens found in each nest. It seems probable that two queens were in nests having 10 and 12 cells, but that one disappeared or was lost in two cases.

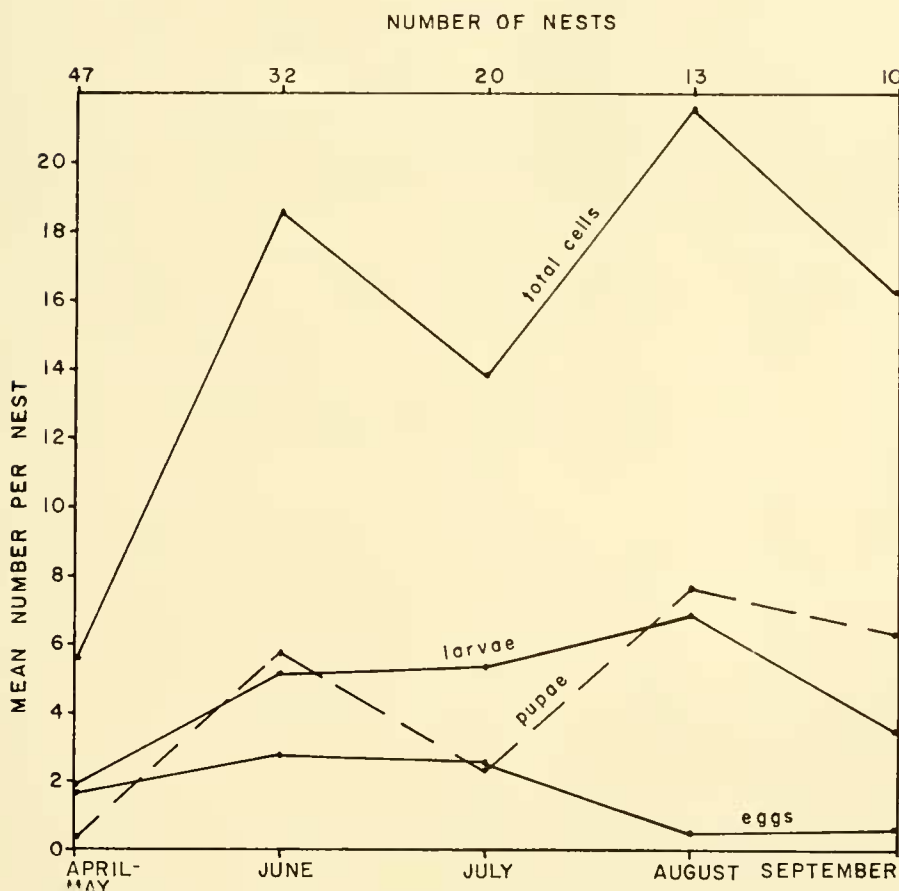


FIGURE 19. Cells and their contents. The excess of the total cells over eggs + larvae + pupae is due to cells under construction and being provisioned as well as old abandoned cells that were not filled with earth. The dip in cell number in July compared to June and August may be a result of small sample sizes or biased sampling resulting from comparing in this figure data obtained in different nesting places and in different years; or it may represent biological fact. However, the only year (1952) for which we have good records for both June and July from the same nesting area suggests that the dip in July did not occur in that place in that year of relatively moist soil [June $\bar{x} = 12.3$ ($n = 22$); July $\bar{x} = 15.6$ ($n = 12$)].

considerable variation. Nests occupied by more than one queen contained correspondingly more cells. The average number of cells per nest was 10.1 (This mean is higher than shown in Figure 19 and Table VI because incomplete nests are included in the latter figure and table).

After emergence of the workers, the number of cells increases, as shown in Figure 19 and Table VI. The maximum number found in any one nest was 90 (Figure 14), found near the end of June, but nests with over 50 cells were found at various times until early September. During each of the summer months nests with only 4 to 7 cells were also found, and even two or three nests without cells. The nests without cells were not new ones, but old ones with earth-filled remnants of cells, but without new ones. The above figures for cell numbers, and those used in preparing Figure 19 and Table VI, exclude old, used cells filled with earth and in-

TABLE VI.—Number of Cells and of Eggs, Larvae and Pupae Per Nest. n = number of nests; \bar{x} = mean; SE = standard error of mean. Under the heading “%” are shown the percentage of the cells that contain eggs, larvae, and pupae.

	n	Number of cells			Number of eggs			
		\bar{x}	SE	range	\bar{x}	SE	%	range
April-May...	47	5.45	.867	0-28	1.81	.574	33.2	0-24
June.....	32	18.56	4.025	1-90	2.78	.891	15.0	0-19
July.....	20	13.75	2.385	4-47	2.65	.956	19.3	0-14
August.....	13	21.62	5.281	0-67	.62	.331	2.8	0-4
September...	10	16.30	4.690	0-52	.70	.422	4.3	0-4

	n	Number of larvae				Number of pupae			
		\bar{x}	SE	%	range	\bar{x}	SE	%	range
April-May...	47	1.92	.375	35.2	0-10	.06	.064	1.1	0-3
June.....	32	5.19	1.493	28.0	0-34	5.84	1.327	31.5	0-34
July.....	20	5.40	1.125	39.3	0-21	2.45	.541	17.8	0-7
August.....	13	6.92	1.806	32.2	0-23	7.69	2.379	35.6	0-23
September...	10	3.50	1.609	21.5	0-12	6.40	3.140	39.3	0-30

clude only those containing immature stages of bees and those in the process of being constructed or provisioned and such old empty cells as exist.

According to the system of Sakagami and Michener (in press) nests of *L. inconspicuum* are to be classified as follows: OChⁿB.

Nest construction: The starting of a new nest by a single queen bee was observed several times in the spring. At this season many of the overwintered queens spend much time crawling over the surface of the ground, flying short distances, alighting here and there, and crawling more, often biting at the ground with their mandibles. Not infrequently they start to dig, but usually after making a hole one or two millimeters deep, they abandon it and continue the activity which looks like searching. This can be observed most readily in areas of nest aggregations but with patience can also be seen in many other patches of bare ground. Sometimes several such bees were seen at the same time in an area where a nest was never subsequently found. Occasionally, perhaps most commonly in the afternoons, such a bee continues its digging, disappearing into the soil in as little as 20 minutes if the soil is moist and easily worked. The digging is done with the mandibles; as the hole becomes deeper earth is pushed out with the posterior-dorsal surface of the abdomen and forms a tumulus which spreads irregularly all around the entrance of the burrow.

As explained previously, dirt excavated in digging new cells or extending the burrows in established nests is often put in old abandoned cells (which rarely stay open long) or in short branch burrows, rather than being carried all the way to the surface. We replaced the upper 10 to 20 cm. of certain nests with glass tubes which had cell-like evaginations blown in them. The bees never used these evaginations as cells but soon filled them with earth brought up as a result of work below the level of the glass tubes. Nonetheless tumuli appear at irregular intervals throughout the summer at the entrance of every nest containing an active colony of bees, for there is never enough space below the surface for all the dirt that is dug out by the bees.

The smooth areas around the nest entrances appear to be made by the bees which act as guards; such areas are absent at the entrances of nests inhabited by only a single bee, and guarding is not observed at such nests. A bee at the nest entrance can often be seen mouthing the smooth area with its labium, and also rubbing it with its front tarsi, which are bent mesad under the head. Special

attention is paid to the rim of the entrance hole, *i. e.*, to the inner margin of the smooth area. The postero-dorsal extremity of the abdomen is often used to shape this region, by patting motions when the soil is moist. Similar patting was sometimes observed to shape the outer margin of the smooth area, as is shown by the following notes made soon after a heavy rain. The smooth area had already been fairly well reformed, but the guard bee was still at work on it. She reversed herself inside the nest and backed out of the nest so that the whole abdomen was exposed and strongly arched so that the tip was directed downward. Supported within the entrance by the outside surfaces of the legs thrust against the walls, the bee tamped the smooth area with the apex of the abdomen, the whole abdomen being moved up and down. Small changes in position allowed the abdomen to tamp different parts of the smooth area. The parts close to the nest entrance were tamped as the bee slowly moved into the nest, and similar tamping continued inside of the nest, smoothing and making more firm the inside wall of the burrow.

It would seem that the diameter of the smooth area is a reflection of how far the bee can reach with the abdomen. Probably the size of various other structures of the nest are also related to dimensions of the bees, the entrance being of a size to admit only one bee at a time, the rest of the burrow being large enough to allow bees to pass one another readily.

When the soil surface is very dry and the smooth area completely gone due to crumbling of the soil, a little water allowed to soak into the soil about the nest entrance is sufficient to cause the guard to construct a smooth area. Sometimes two or three bees will work at and just inside the nest entrance simultaneously, patting with their abdomens to shape the entrance and its smooth area.

Because of the relatively uniformly colored soil in the areas of our study, we did not readily detect the working of the soil forming the lining of the burrow. Soil from deep in the nest lines the burrow to the surface in many halictine bees and *L. inconspicuum* is probably not an exception. At least this species has the ability to construct burrow linings of soil, for if we replaced the upper part of a nest with a glass tube slightly too large in diameter, or if we installed a glass window in the side of a burrow, the bees promptly lined the tube or window with soil, patting it into place with the dorso-apical part of the abdomen. This covering was much less

likely when the glass was covered (except at the times of our observations) to prevent light from entering the burrow.

If the constriction of the burrow at the surface of the ground was destroyed, then the bees would narrow the entrance again by bringing soil from deep in the nest and forming a lining around the entrance of the burrow.

Through the glass windows and tubes, as well as by observations of undisturbed nest entrances, it was possible to see that the bees bring dirt up from deep in the nest either by backing upward pushing the dirt with the dorsal apical part of the abdomen, or by moving upward head foremost, pushing the dirt with the face, especially the clypeus.

In queen nests occupied by single individuals, the uppermost cell is usually the first provisioned, and provisioning continues downward. The result is that as in Figure 6, there is usually a sequence in ages of the immature stages from oldest above to youngest below. This is not invariable, however, for sometimes a pupa will be found below a larva, for example. In nests occupied by several queens this order may persist, but more often does not. Thus in the upper right-hand branch of the nest shown in Figure 7, the mixture of eggs and small larvae is quite complete. Because of the progressive deepening of the burrow and of the level where new cells are made, the same sequence, from older above to younger below, occurs in most nests in summer and fall, when the colony contains workers. However, these nests are usually full of irregularities in the order of the cells, as can be seen in Figure 16 and, to a lesser extent, in several other illustrations.

Most nests in which cells are being constructed and provisioned have one or two complete cells ready to be provisioned, as indicated by the letter "E" on the diagrams of nests. This is true even of small insects, such as queen nests made by single queens in the spring. Contrary to many bees which make, provision, and seal a cell before starting to make the nest, *L. inconspicuum*, while provisioning one cell, seems to be making one or two others. This is true of most Halictinae (see Sakagami and Michener, in press).

Provisions and Immature Stages: In opening nests one occasionally finds fresh cells containing a mass of loose pollen on the floor (Figure 20, a). Sometimes a small lump has been moistened, presumably by honey, and hence forms an irregular firm mass. When the provisions are complete, however, there is virtually no dry pollen in the cell; all of it is worked into a smooth mass. This

mass of provisions has the form of a flattened sphere (Figure 20, b), 1.9 to 2.5 mm. in horizontal diameter and 1.4 to 2.0 mm. in vertical diameter. The egg is white, curved, 1.33 to 1.50 mm. long about .25 mm. thick (Figure 20, b), and is supported by its two ends on top of the mass of provisions. The larva feeds down into the upper anterior* part of the pollen mass (Figure 20, c, d, e), finally turns over with what is left of the pollen mass (Figure 20, f). After the larva has eaten all the food it lies with its head toward the anterior end of the cell. The feces are then voided as soft pellets pushed against the upper posterior portion of the cell, where they form a firm layer (Figure 20, h; Figure 43). Voiding of the feces took

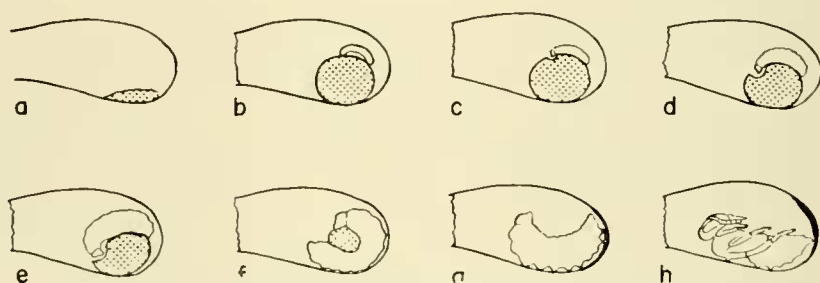


FIGURE 20. Diagrammatic sagittal sections of cells of *Lasioglossum inconspicuum*. a, loose pollen placed on floor of cell; b, mass of provisions with egg on top; c, d, e, f, larva in different growing stages; g, prepupa; h, pupa.

a day and a half for specimens in the laboratory. The larva, at this stage, straightens out and becomes a prepupa, and ultimately a pupa.

We have not done much work on the duration of the developmental stages. We have found it difficult to rear the larvae in the laboratory. We were repeatedly successful in rearing prepupae through the pupal stage to adults but the younger larvae died. The data given below are based entirely on females (probably workers). The duration of the pupal stage varies enormously with temperature; probably that of the other stages varies equally. Prepupae taken on May 10 pupated on May 12; the eyes of these pupae were black 10 days later and adults emerged after another 8 to 9 days; thus the entire pupal stage at room temperatures of 70° to 75° F. required 18 or 19 days. By contrast, another group of prepupae pupated on June 12, and developed at a time when the room temperature in which they were kept ranged from 90° to 95° F. These pupae had black eyes three days after pupation and adults emerged

* Here and elsewhere the words anterior and posterior are applied to cells and structures therein with reference to the orientation of the egg. Probably in all bee cells the anterior end of the egg is toward the orifice of the cell, i. e., toward plug that is made from the outside by the mother bee as she closes the cell.

three days later, so that the total pupal stage required only six days, or about one third of the time required by the group mentioned previously. Obviously the rate of development will vary widely according to weather and the depth of the cells. When pupae were reared at temperatures of 81°-83° F., this stage required eight or nine days; this is probably a reasonable estimate of the duration of the pupal stage in summer.

Among 70 nests fully excavated during June, July, and August, we found totals of 159 eggs, 354 larvae (including prepupae), 324 pupae and 31 teneral adults with milky wings, still in their natal cells. By omitting vernal and autumnal nests from this tabulation, we have avoided the spring nests that have not yet had time to produce pupae and the autumn nests that lack eggs and young larvae while containing many pupae. The total numbers of individuals of the various stages given above ought to be proportional to the duration of the stages. If this be so, the egg stage is a little less than half as long as the pupal stage or perhaps four days, the larval stage is perhaps slightly longer than the pupal stage, say nine days, and the teneral adult remains in its cell for a period less than one tenth as long as the pupal stage, that is somewhat less than one day. This would give us a total of about 21 days from egg laying until emergence of the adult from its cell under summer conditions.

The interval between the average date when pollen collecting was first seen in the spring and the average first date when workers were seen at the nest entrance is 43 days. This period must be roughly comparable to the egg laying to emergence period discussed in the preceding paragraph although pollen is collected and a cell provisioned before the egg is laid; the 43-day period is about twice the estimated summer developmental period of 21 days. This corresponds nicely to the observed duration of the pupal stage in May (18 or 19 days), which was about twice the observed duration of this stage at 80° to 83° F. (8 or 9 days). As indicated in a later section on "Behavior of Queens," observations of individual nests in the field suggest an egg-laying to adult period of about 30 days in the late spring.

INDIVIDUAL AND SOCIAL BEHAVIOR

Aggregations of Nests: As stated previously under "Distribution of Nests," many of the nests are isolated. On the other hand, many are in loose aggregations. Nests were found in relatively few of the apparently suitable areas and aggregations in even fewer.

Usually nesting aggregations do not occupy all of the apparently suitable areas of soil in which they occur. It is not clear why the aggregations occur, in view of the apparent success of isolated nests elsewhere and the abundance of seemingly suitable soil. The areas of concentration are not necessarily areas of successful nesting; we have seen whole aggregations disappear, probably due to death of bees. The same sites are often attractive spring after spring, and many queens establish nests in areas of nest aggregations, even though few nests may have survived the summer in those places. Possibly the odor of nests or bees attracts others to the same vicinity; perhaps a factor contributing to development of aggregations is a tendency of the young queens to return to the vicinity of birth to make new nests.

Nest Populations: The number of adult female bees in one colony (*i. e.*, one nest) varies from one to 25. Most queen nests in the

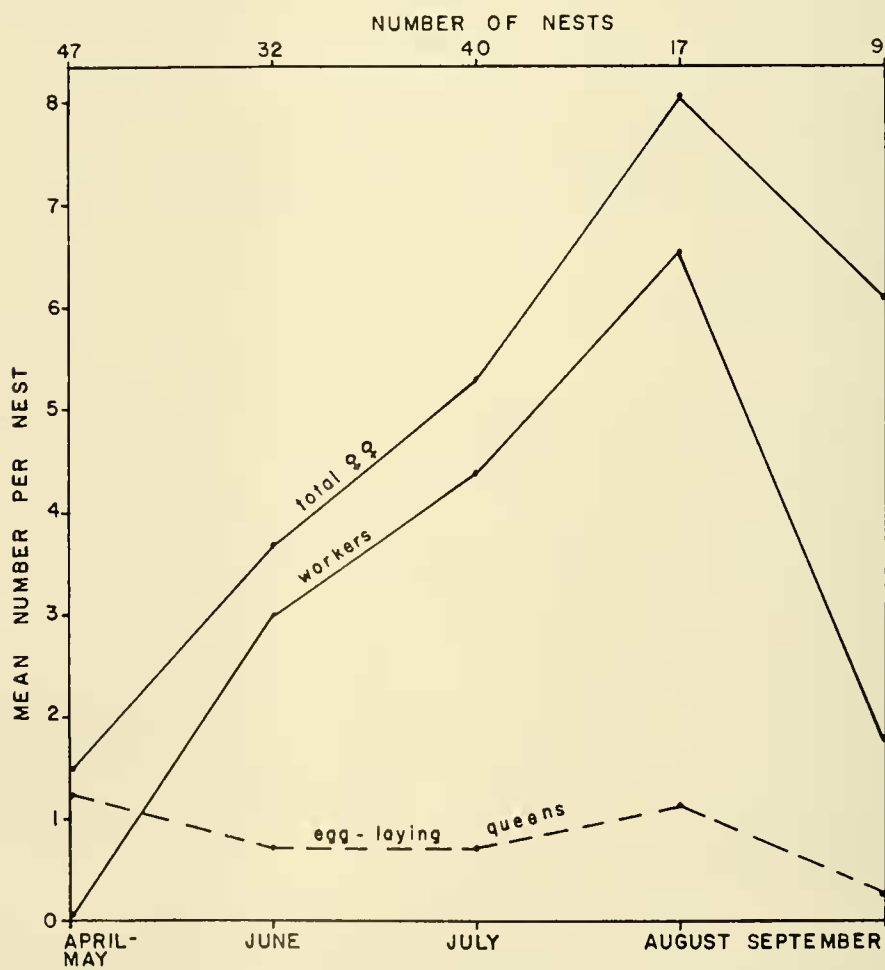


FIGURE 21. Number of adult females per nest. Egg-laying queens (groups A and B) were recognized by dissection. The excess of the total over workers (groups C and E) plus queens is due to individuals that were doubtful as to caste as well as, particularly in September, to young queens (group D). The meaning of the lettered groups is explained later in the text.

spring contain only a lone queen, although we have studied nests at that season inhabited by as many as six queens (Figure 18). With the production of workers, the population of adults in the nest rises, reaching a peak in August (Figure 21, Table VII) of over eight females per nest, on the average. This average total, of course, includes numerous small colonies, for throughout the season many colonies die out, and during the process they often reach the stage of having only one or two bees each.

TABLE VII.—Number of Adult Females Per Nest. n = number of nests; \bar{x} = mean; SE = standard error of mean. Queens were fertilized egg-laying individuals; workers were usually unfertilized and had not over one or two enlarged oocytes; other females were doubtful as to caste or were young queens. The meaning of groups A, B, C, D, and E, is explained in the text later. The number of nests shown here is more than indicated in Table VI and related materials because of nests whose populations were preserved but for which data on cells, etc., was not recorded.

	n	Queens (groups A and B)			Workers (groups C and E)			Other females (group D and ungrouped)		
		\bar{x}	SE	range	\bar{x}	SE	range	\bar{x}	SE	range
April-May..	47	1.21	.161	0-6	.09	.053	0-2	.19	.072	0-2
June....	32	.72	.138	0-3	3.00	.803	0-16	0		
July....	40	.70	.090	0-2	4.48	.475	0-14	.18	.062	0-2
August..	17	1.18	.182	0-3	6.65	1.654	0-22	.24	.106	0-1
Septem-ber...	9	.22	.147	0-1	1.78	.782	0-6	4.11	1.505	0-15

Males: The occurrence of males during the season is indicated in the section on the seasonal cycle. Males leave their nests soon after emerging from their cells; therefore the few males found in the nests do not give a correct idea of the proportion of males produced. Figure 22 shows the percentages of the young produced at various seasons that are males. In contrast to *L. rhytidophorum*, (see Michener and Lange, 1958) there is no clear peak of male production in spring. Instead, in May and early June no males seem ordinarily to be produced. Males have been recorded, as indicated in the section on the "Seasonal Cycle," as early as June 1 (two different years) and June 10. Unfortunately these early males have not been preserved and it is now apparent that they might

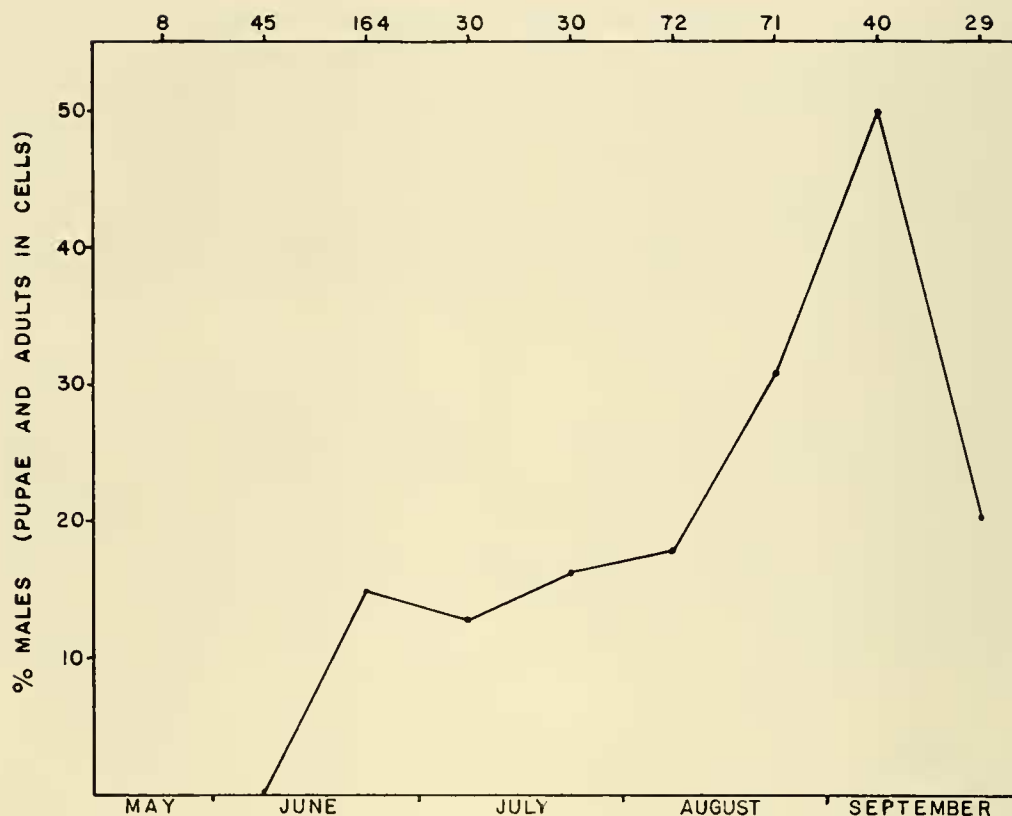


FIGURE 22. Graph showing percentage of pupae and of young adults (in closed cells) that are males. Each month is represented by two points, one for the first half, one for the second half. The number of pupae and young adults examined during each period is shown at the top of the graph.

have belonged to *Lasioglossum* (*Paralictus*) *cephalotes*, a parasite in the nests of *L. inconspicuum*.

Most of the males indicated in Figure 22 were produced in nests which were also producing females. However, two nests were found which were producing only males. On July 15, 1951, a nest was opened containing five male pupae but no eggs nor larvae. The nest had been marked on June 6, at which time it contained at least two foraging workers. By July 15 it has been long closed by rains and was unrecognizable at the surface of the ground. It seems possible that the founding queen died, that her unfertilized workers laid at least five eggs, and that after the workers died these males continued their development.

The other nest which produced only males was opened on June 21, 1952. It contained seven male pupae as well as three larvae of unknown sex and three adult females. Two of the latter were workers, both with very slender ovaries while one was a queen; unfortunately her spermatheca was lost and we do not know if she was mated or not. However, she was probably the mother of the

workers. She contained no very large oocytes (longest .91 mm.), not a surprising finding since the nest contained no eggs or small larvae. The reason for this nest producing males at this season is unknown.

Males visit flowers for nectar but are most often seen flying about the nesting areas. At a nesting area like that at Potter's Lake where the vegetation (except for large trees) is very low, the males zig zag over the soil or small plants, usually flying from two to 12 cm. above the ground. Where there is higher vegetation, they fly higher, often flying in numbers around the weeds at altitudes as high as one meter. In Riverside, California, where *L. inconspicuum* has been introduced, around the home of Mr. P. H. Timberlake, males were noted in immense numbers flying rapidly about small trees in the nesting area; although there were more at heights of one or two meters, some could be seen around foliage five meters above the ground.

When males are scarce, individuals often make these flights alone but when they are numerous they usually dance in loose groups, each individual zigzagging with great rapidity. Often one or a few will alight on the ground or foliage over which they are flying, only to resume flight in a few seconds or minutes. Flights such as this, in the vicinity of nests, are usually in the sun when the temperature is moderate but in the middle of the day on hot days, when the temperature in the shade rises above about 100° F., the flights move into partially shaded areas. At open nesting sites where there is no shade from weeds or nearby trees, the flights cease and the males disappear during the warmest hours of hot days.

We are not sure whether we have observed mating or not. Males, sometimes two to four of them simultaneously, often pounce on females. Usually they are repulsed immediately, often only after rolling over on the ground, but sometimes contact lasts for about 10 seconds; this may be copulation. Males pounce upon any halictine of about the right size. Young females and old senile females that fly about the nesting area unable to find their nests are most commonly pounced upon by males, but foragers at nearby flowers, males of other species of *Chloralictus*, and females of the parasite, *L. (Paralictus) cephalotes*, are all often attacked. Since such activity has been noted on the ground, on foliage, and on flowers; we assume that mating may occur at any of these places. We believe that it usually occurs near the nesting site rather than on distant foliage or flowers.

It is significant that males collected on flowers varied in mean size according to the season. It has been shown elsewhere (Michener and Lange, 1958, 1959) that wing length, face width, and other body measurements in halictine bees are highly and positively correlated so that any one can serve as a fair index of size. Facial width and wing length were measured for series of specimens collected in different months as shown in Figure 23. For both measurements the mean for July males was below means for June and September (difference significant at the 5% level; Q test, Snedecor, 1956, p. 251); differences between the June and September means were not significant. Only small numbers of specimens were available for August; they were intermediate in mean size between the July and September series. As will be shown later, the seasonal

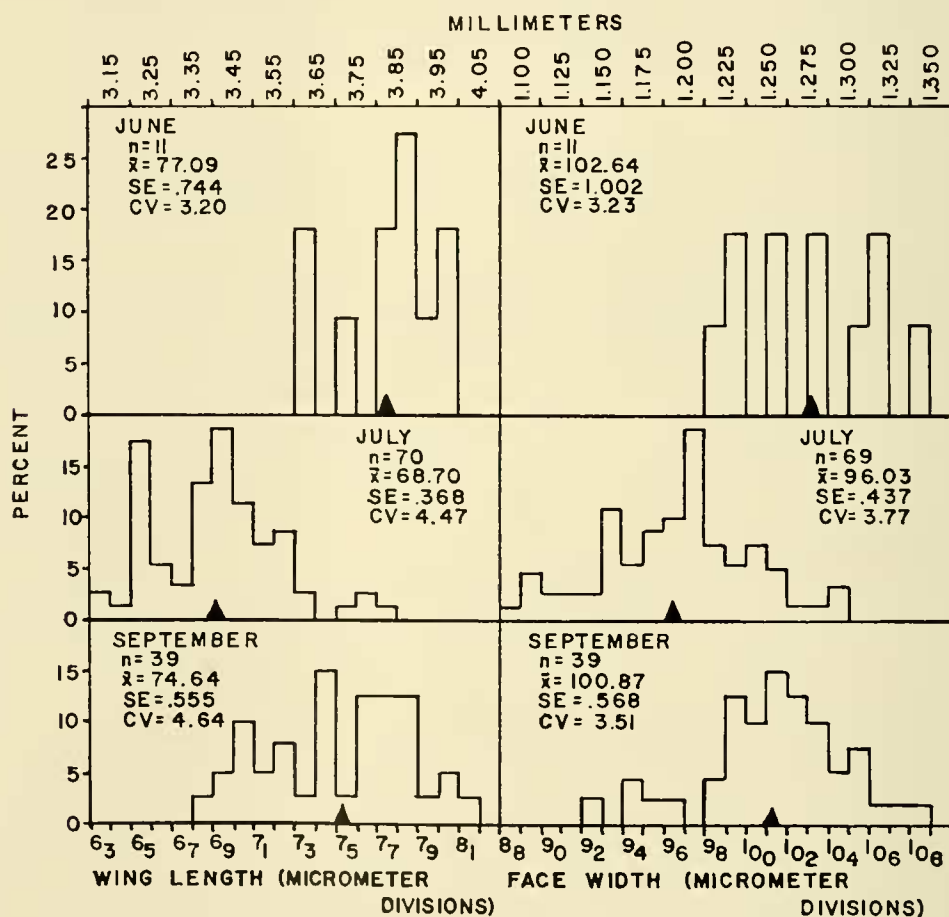


FIGURE 23. Histograms showing wing lengths (left) and head widths (right) of males of *Lasioglossum inconspicuum* collected on flowers in the months of June, July, and September. Statistics are shown in micrometer divisions with equivalents in millimeters across the top. The means are marked by black triangles at the bases of the histograms. Abbreviations; n = number of individuals measured, \bar{x} = mean, SE = standard error of mean, CV = coefficient of variation.

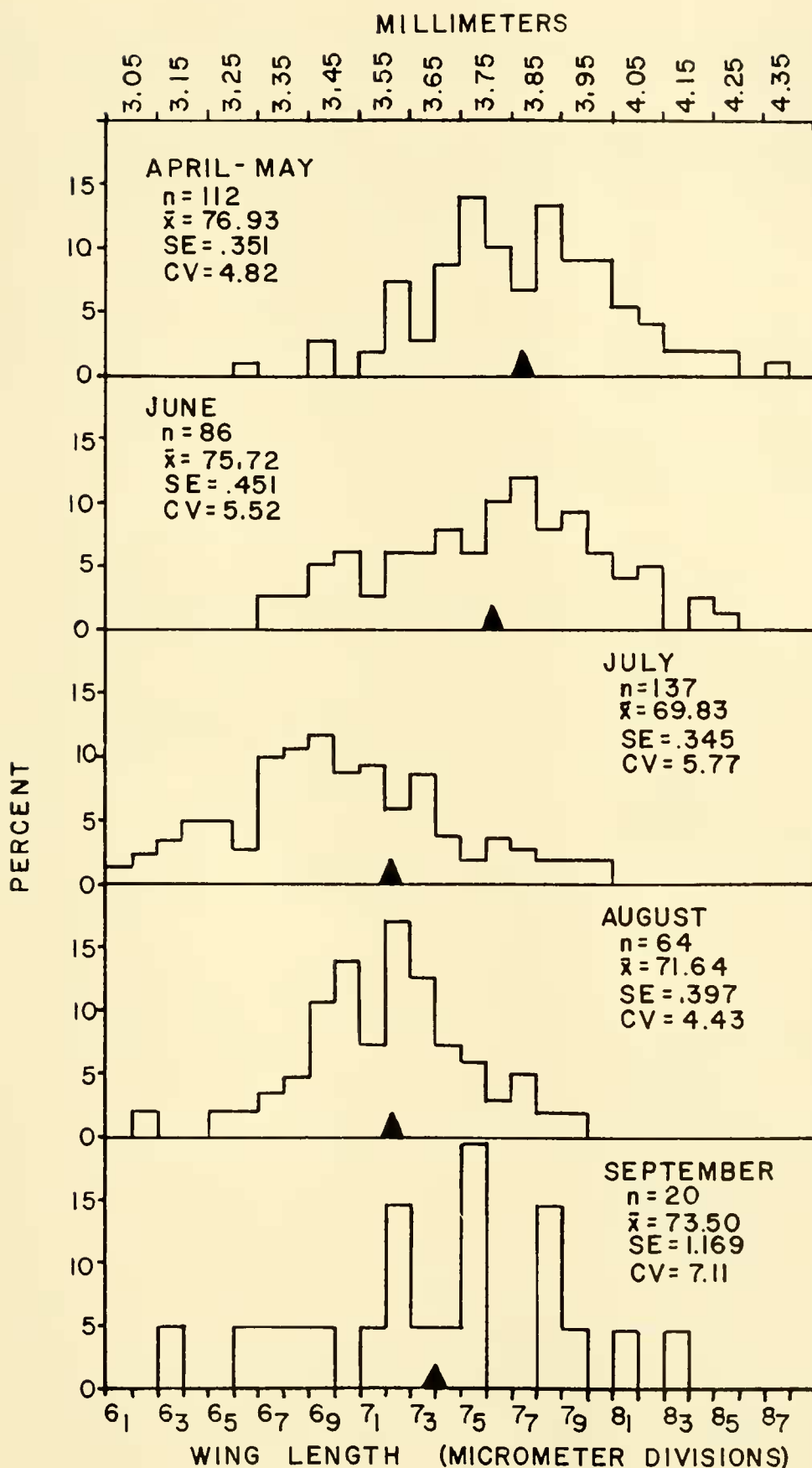
size variation of the males is positively correlated with that of females.

Variation in Size Among Field-collected Females: Females, like males, collected on flowers varied in mean size according to the season, as shown in Figures 24 and 25. Minimum size occurred in July as determined by wing length, in August as judged by head width. To judge by observations of nests, the April and May individuals should all be queens, the June, July and August individuals should nearly all be workers, while those taken in September should be a mixture of workers and young queens. The relatively low means for September (as compared to April and May), and the high coefficients of variation for that month, must be due in part to the mixture of workers and young overwintering queens on the flowers during that month. The young queens that actually overwinter are the same individuals that visit flowers in April and May and should, of course, be of the same size unless there is differential mortality of smaller individuals.

The means shown in Figure 24 are significantly different at the 5 percent level (a posteriori Q tests among means, Table 29, upper 5 percent, Pearson and Hartley, 1956) except that September is not significantly different from June and August, and June is not significantly different from April and May. The means shown in Figure 25 are significantly different at the 5 percent level by the same method except that July and August are not significantly different from one another or from September, and June is not significantly different from April and May.

Caste Differences: The interpretation suggested in preceding sections indicates the presence of more or less different female castes (queen, worker). In order to study the castes, entire populations from over 150 nests were captured and dissected. Occasionally a bee escaped, but insofar as possible complete nest populations were obtained (1) by excavating in cool cloudy weather when no bees were afield; or (2) by plugging nests that were to be opened either at night or during other hours when all the bees were presumably in the nest; or (3) by watching a nest for one and one half hours or more before excavating it, in order to capture returning bees, meanwhile preventing the departure of all individuals from the nest. All individuals from such nests were dissected to determine ovarian development, presence of pollen in the crop, and of sperm cells in the spermatheca.

FIGURE 24. Histograms showing wing lengths of females of *Lasioglossum inconspicuum* collected on flowers in various months. Statistics are shown in micrometer divisions with equivalents in millimeters across the top. The means are marked by black triangles at the bases of the histograms. These measurements cannot be compared directly with wing measurements in subsequent tables for the wings were measured by a different person and in a different manner. Abbreviations: n = number of individuals measured, \bar{x} = mean, SE = standard error of mean, cv = coefficient of variation.



On the basis of ovarian development and presence or absence of sperm cells in the spermatheca, females can be divided into several groups as follows:

A—Fertilized, with ovaries much swollen, usually to the point that enlargement of the posterior portions of one or both ovaries often forces the anterior portions of one or both into sharp bends or convolutions (Figure 26). Such ovaries seemed more swollen than in the corresponding class of *L. opacum* and *rhytidophorum* (Michener and Lange, 1958), as would be expected since the first is a nonsocial species and the second has shorter-lived queens than those of *inconspicuum*. No doubt *inconspicuum* queens produce more eggs than those of either of the aforementioned species of *Chloralictus*. The ovaries of none of these species are nearly as large, however, as those of the species with perennial nests and large colonies (Plateaux-Quénu, 1959).

B—Fertilized, with ovaries swollen but not so much as in Group A, not sharply bent, usually one or two ovarioles in each ovary not swollen (Figure 27).

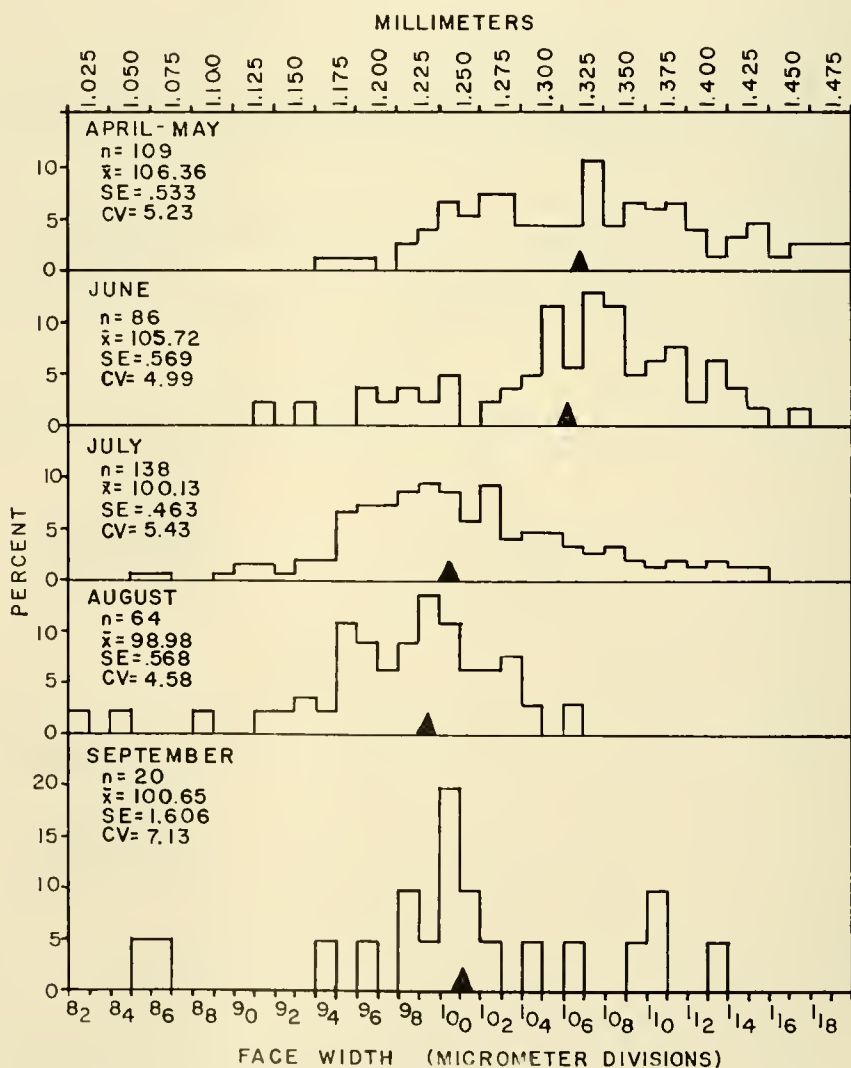
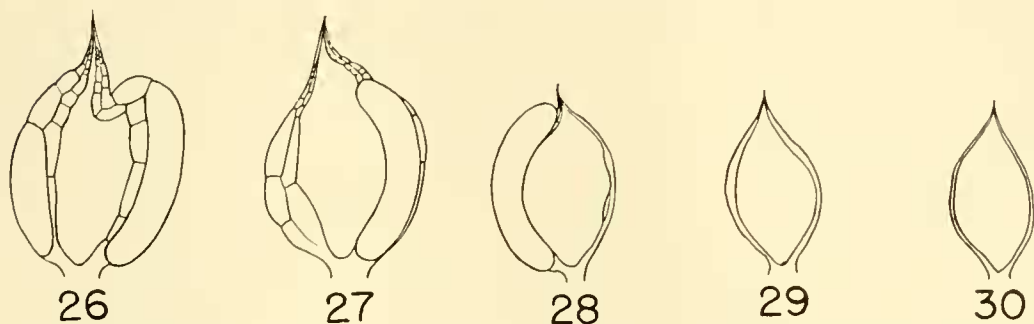


FIGURE 25. Histograms showing head widths of females collected on flowers in various months.

C—Unfertilized, with ovaries slender except for one enlarged oocyte in one ovary, or rarely one in each (Figure 28).

D—Fertilized, with slender ovaries.

E—Unfertilized, with slender ovaries. Because so many bees fell in this group, it was decided to divide it into two arbitrary subgroups for separate analysis. These were E' with very slender ovaries (Figure 30) and E'' with merely slender ovaries (Figure 29).



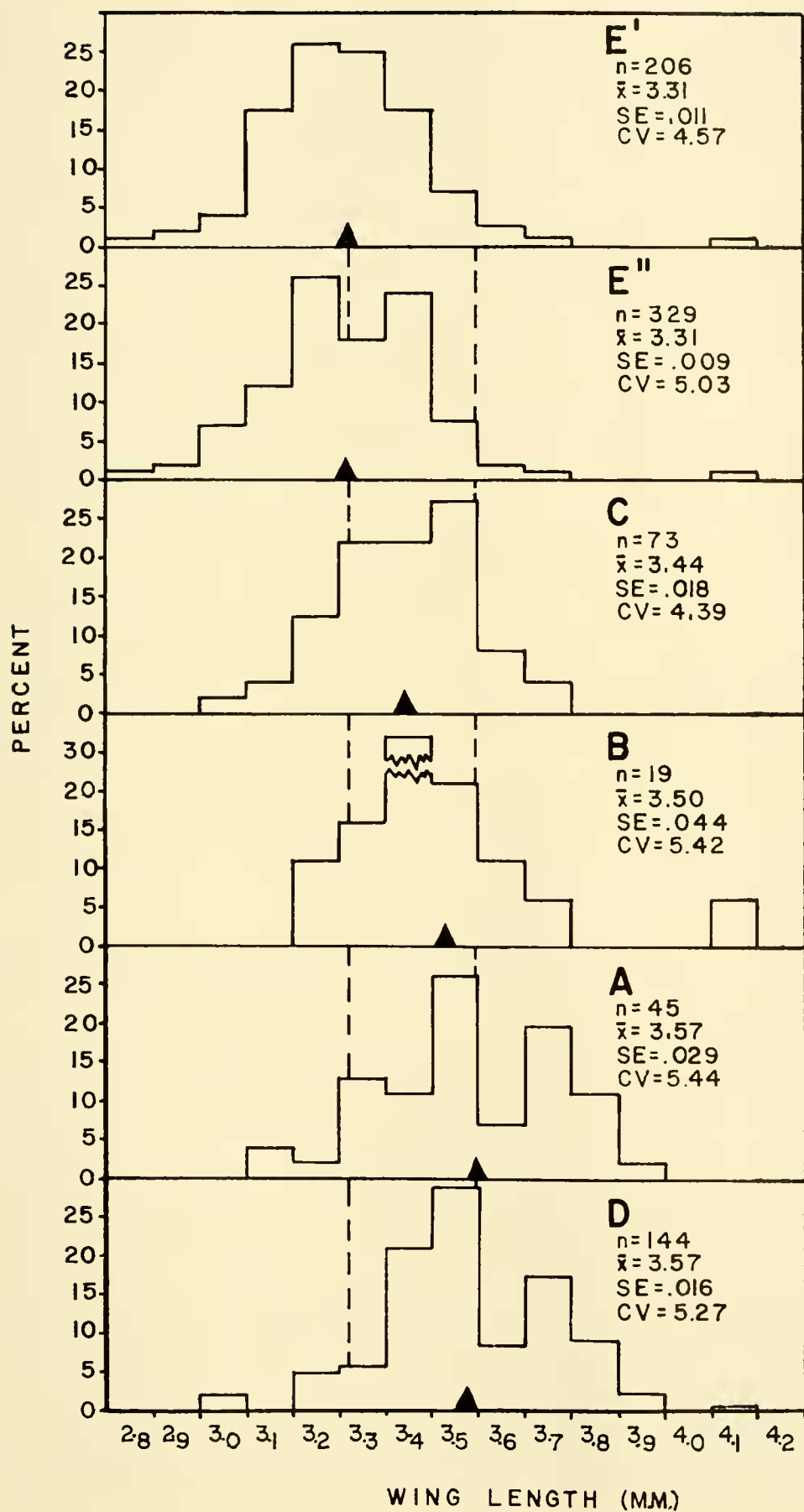
FIGURES 26 to 30. Ovaries. 26, group A (queen); 27, group B (queen); 28, group C (worker); 29, Group E'' (worker); 30, group E' (worker).

From the standpoint of ovarian size, the groups merge. All females emerge from their pupae as Group E'. Some remain in that condition while others develop into one or another of the other groups. It is therefore to be expected that intermediates would occur. There is also excellent evidence that ovarian size may be reduced, so that progress from A to B may occur but probably not as far as D. If a group C female lays an egg she would revert to group E. Peculiarly-shaped ovaries with irregular swellings or with a developing oocyte that is much shorter than normal occur occasionally. Such individuals were placed rather arbitrarily in the classification indicated above.

In a certain percentage of individuals dissected the spermatheca was missed, or lost before it could be examined for the presence of sperm cells. In some cases such specimens were included in the analyses which follow. For example, since virtually every individual taken in April and May is fertilized, such specimens were included in group A or B even if proof of fertilization was not obtained.

Figure 31 shows the sizes (wing lengths) of females segregated into the groups listed above. In view of the seasonal cycle of the species and the differentiation of castes explained below, and to make the groupings more biologically significant, group D is limited for purposes of Figure 31 and related discussion to individuals obtained from October to May (overwintering or overwintered queens) while the other groups are limited to individuals taken in June, July, or August. In this species there are very few fertilized

FIGURE 31. Histograms showing wing lengths in millimeters of females belonging to groups A to E. These are groups based on ovarian development and presence or absence of sperm cells in the spermatheca, as indicated in the text. The histogram for group D is based on specimens taken from October to May; the other histograms are based on specimens taken from June through August. Means are shown by triangles on the base lines. The vertical broken lines are only to facilitate comparison and represent the minimum mean (group E') and the maximum mean (group A).



workers; therefore there is no large number of group D individuals in summer, as in *L. rhytidophorum*.

It is apparent that, correlated with the functional differences responsible for segregation of individuals into groups A to E, there exist certain size differences, as indicated by measurements of wing lengths. There are not, however, external morphological differences between the female castes as in bees like *Trigona* and *Apis*.

No difference in size exists between groups E' and E". These constitute the typical workers. Group C consists of workers which may lay one or more eggs. Their mean size is larger than that of workers with slender ovaries. The difference is significant at the one percent level (Q test, a posteriori, among means, Table 29, upper one percent, Pearson and Hartley, 1956). The remaining groups consist of queens. Group D, consisting almost entirely of overwintering females, should represent queens as a whole; its mean size (as measured by wing length) is significantly different from that of group C at the one percent level. During the active season queens are divided into two groups, A and B, according to ovarian size. Those falling in group A have a mean wing length slightly but not significantly larger than those falling in Group B. The mean wing length of groups A and B are not significantly different at the 5 percent level (Q test, a posteriori, among means, Table 29, upper 5 percent, Pearson and Hartley, 1956) from that of group D. The mean wing length of group B is not, but that of group A is significantly different from that of group C at the 5 percent level.

Since queens average larger than workers, one might suspect that in any one nest the queen would be larger than the workers which must usually be daughters of the queen. While this is more often true than not, nests were commonly found in which one or more of the workers was larger than the queen or queens. In June 77.7 percent of the nests studied had the queen (or at least one of the queens in nests containing more than one) larger than any of the workers. In July and August comparable figures were 65.2 percent and 58.3 percent, respectively. That the queens average larger in June than in July and August, probably because of replacement of some or many overwintered individuals, is suggested in the section on "Seasonal Differences in Size," and would explain the progressive reduction in the percentages shown above.

There is no correlation between worker size and colony size in this species.

It is noteworthy that in this species the smallest workers are

smaller than the smallest queens. This is not true of *L. rhytidophorum* in which the entire range of size variation of the workers overlaps that of the queens, although the largest queens are larger than the largest workers (see Michener and Lange, 1958). Thus it seems that the differentiation of the castes from the standpoint of size is more complete in *inconspicuum* than in *rhytidophorum*, a conclusion that is not surprising in view of the greater differentiation of the castes from the viewpoints of longevity and ovarian development. That there is no necessary correlation among various kinds of caste differences is shown, however, by Plateaux-Quénu's (1959) study of *Lasioglossum marginatum*, a species with queens and workers well differentiated in behavior, longevity, etc., but equal in size. Unfortunately suitable statistical data are not available for such well-studied species as *L. malachurum*.

Seasonal Differences in Size: It is evident that part of the seasonal variation in size shown in specimens caught on flowers (Figures 24 and 25) is due to the caste differences correlated with ovarian size and mating. Overwintering individuals are all queens (group D). In April and May they are the bees making and provisioning new nests. In the fall new overwintering individuals are produced. In the months of June through August, most of the individuals on flowers are workers (groups C and E). It is therefore not surprising that spring and fall individuals taken on flowers are larger than those taken during the summer. However, during the summer months differences were also noted among the monthly mean wing lengths of field caught specimens and some of the monthly means were significantly different from others.

In order to elucidate such variation during the summer, seasonal size variation of bees removed from nests and segregated as to group was investigated. The results are shown in Table XIII. Group B is excluded since it is represented by so few individuals; group D does not appear in the table since virtually all bees of that group (all those utilized in Figure 31) were overwintering or overwintered queens. It is evident from Table XIII that the June individuals average larger, July and August ones smaller. This fact is particularly noteworthy among queens (group A), where the August individuals average larger than those taken in July, and among workers with one or two large oocytes (group C), where the August individuals average smaller than those taken in July. The differences between monthly means for group C are statistically significant at the one percent level and the difference

between June and July means for group E are significant at the five percent level. The consistently larger size in all lettered groups for June than for July and August, considered with like fluctuations in field caught females (Figures 24 and 25) and males (Figure 23), makes reasonably clear that June individuals of each lettered group do average larger than those taken in July and August.

The mean sizes of individuals with unworn mandibles (presumably young adults) (last column, Table VIII) practically do not vary from month to month. Presumably most of these individuals would become group E workers. Note the similarity of

TABLE VIII.—Wing Length (mean and their standard errors) of Females Belonging to Various Groups (explained in text). Not all were taken from nests. Comparable data on unworn and presumably young individuals obtained from nests during the summer months are given in the last column. The numbers of individuals examined are shown in parentheses.

	E	C	A	Unworn
June.....	3.36 ± .028(60)	3.56 ± .033(15)	3.65 ± .051(15)	3.31 ± .045(28)
July.....	3.30 ± .010(265)	3.45 ± .029(23)	3.50 ± .045(18)	3.29 ± .016(105)
August...	3.31 ± .010(210)	3.39 ± .024(35)	3.58 ± .051(12)	3.30 ± .018(59)

their mean wing lengths to those of group E workers shown in Figure 31. There is evidence presented below (section on "Behavior of Workers") showing that such workers are short lived; it is therefore not surprising, since they not only constitute the bulk of the population but also must constantly be replaced, that the bulk of the summer production is of such workers. Evidence presented below shows that queens and perhaps workers with one or two enlarged oocytes (group C) live longer than group E workers. To appear in summer collections from nests, therefore, such individuals would not need to be produced in very large numbers. The group C workers (plus perhaps various potential group C individuals, as well as group C workers that have just laid an egg and hence look like group E, and intergrades between groups C and E) visit flowers, although queens rarely do so in summer. It seems likely that the monthly fluctuation in mean size of field caught individuals results largely from such workers with reproductive tendencies, which, together with the queens, seem to average distinctly larger in June than in July or August if Table VIII is meaningful.

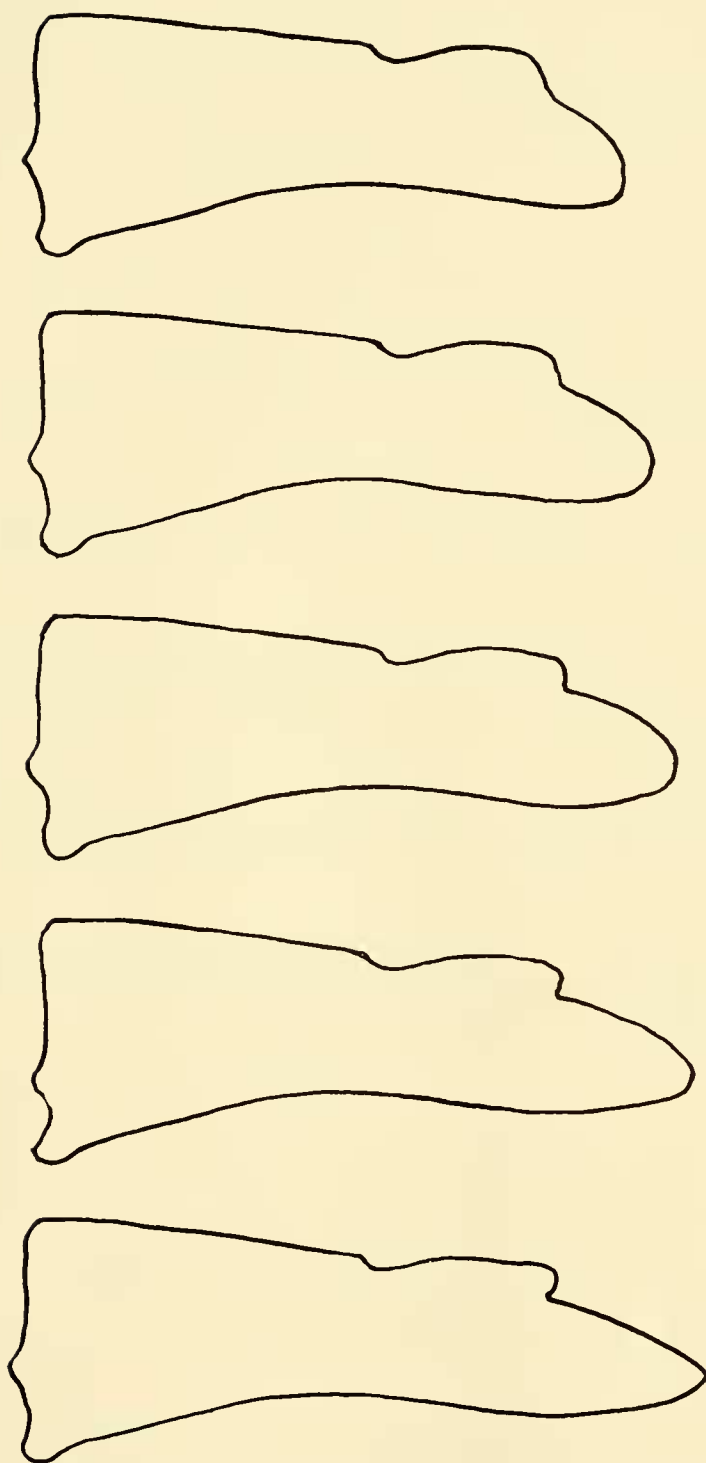


FIGURE 32. Mandibles of females showing typical examples of the five degrees of wear utilized in the analysis of activity. The indices of wear used are 1, unworn (below); 2, slightly worn; 3, well worn; 4, much worn; 5, very much worn (above).

The large size of the June queens (group A, Table VIII) compared to the overwintering queens (group D, Figure 31) may indicate differential survival of the largest queens. The smaller mean size of the July and August queens (Table VIII) may indicate that replacement queens of average size for queens (group D, Figure 31) have been produced in at least some of the nests during the summer.

Queens: The percentage of females belonging to each group at various seasons of the year is shown in Table IX. This table is based entirely on material from excavated nests. It is apparent that overwintering occurs almost entirely as fertilized females (queens) with slender ovaries (group D). The only exceptions found to this statement were three unfertilized individuals (group C) that must have overwintered and were found in different nests in April, 1955.

Because the wings are rarely nicked in this tiny species, the index of wear, unlike that used for other halictines in previous publications, is based entirely on the mandibles (1, unworn; 2, slightly worn; 3, well worn; 4, much worn; 5, very much worn; see Figure 32). The index of wear therefore reflects the amount of digging in the ground done by the bees. As shown in Table X, the overwintering bees are unworn or nearly so.

TABLE IX.—Percentages of Females Belonging to Groups A to E During Various Months. All specimens were taken from nests (data for April were obtained in the last half of the month).

	Number of bees	Percent in each group				
		A	B	D	C	E
April.....	35	42.9	37.1	11.4	8.6
May.....	45	42.2	33.3	17.8	6.7
June.....	103	18.5	3.9	12.6	65.1
July.....	213	9.0	4.7	1.4	5.7	79.7
August.....	131	9.2	6.1	3.8	6.1	74.8
September.....	59	1.7	1.7	57.6	1.7	37.3
October.....	17	100.0
November- December.....	14	100.0

By the second half of April, 80 percent of the individuals obtained had enlarged ovaries (groups A and B) as shown in Table IX. The time of emergence from overwintering quarters appears to be highly variable, for we have seen new nests established from early April to mid-May. Nests seen and excavated by us were nearly all open ones; we would have missed any closed ones still containing hibernating bees. Therefore it is probable that less than 80 percent of the total female population develops enlarged ovaries by the second half of April. This belief is supported by the relatively high percentage of bees still having slender ovaries in May (group D, Table IX) and by the not or little worn mandibles of many bees in May (Table X).

The sharp reduction in the percentage of queens (groups A and B) in the population in June and subsequent months (Table IX) is due to the large worker populations (groups C and E). The number of queens per nest decreases only slightly and gradually through the summer months, as shown in Table VII and Figure 21, which are based for the most part on data from the same nests as Tables IX and X.

Table X shows that the average indices of wear for queens during the summer are high, probably in group A progressively higher as the summer months pass. Table XI, giving the raw data for group A and B queens lumped together, shows this trend more clearly. This trend seems to indicate that some of the overwintered queens live through much of the summer. It was our impression as specimens were dissected that at least through June and probably well into July and perhaps August, the queens that we found were mostly overwintered individuals. Survival of queens through most of the summer would also be expected since most males appear in late summer and fall, they mate with young queens that will overwinter. If replacement of the queens in nests were a general or universal event, for example in midsummer, males would be expected to be as abundant in midsummer as in late summer and autumn.

Table XI shows that scattered unworn and slightly worn queens were found in nests through the summer months. Table X shows that most but not all of these few queens were of group B; it also shows that a few not or little worn, fertilized bees with slender ovaries (group D) were found in July and August. Such bees can only be regarded as young queens produced in summer, perhaps to replace ineffective or dead overwintered queens. Figure 33 shows

TABLE X.—Indices of Wear of Females Belonging to Groups A to E During Various Months. All specimens were taken from nests (data for April were obtained in the last half of the month). Each entry consists of the mean index of wear, the extremes in parentheses, and the number of specimens examined. From May to September data are given for each half month instead of on a monthly basis.

	Mean (and extremes) indices of wear, followed by N				
	A	B	D	C	E
April	2.9(2-4) 15	2.8(2-4) 13	2.5(2-3) 4	3.3(2-4) 3	
May	1.5(1-3) 16	2.1(1-3) 9	1.6(1-4) 8		
	3 (3) 2	2.3(2-3) 3			1 (1) 3
June	3.3(2-5) 8	2.0(1-3) 2			1.5(1-3) 22
	3.6(2-5) 11	1 (1) 2		2.2(1-5) 13	1.8(1-5) 45
July	3.2(2-4) 9	4.2(4-5) 5		3.0(2-4) 5	1.6(1-5) 112
	3.6(1-5) 10	3.2(2-5) 5	2 (1-3) 3	3.4(1-5) 7	2.2(1-4) 58
August	4.2(3-5) 6	2.8(1-4) 5	1 (1) 3	2.8(1-4) 4	1.9(1-5) 73
	4.7(4-5) 6	4.0(3-5) 3		3.2(2-5) 5	2.1(1-4) 25
September	5 (5) 1		2.9(1-5) 7	3 (3) 1	2.7(1-5) 17
		(4) 1	1.1(1-5) 27		1 (1) 5
October			1.1(1-2) 17		
November-December			1 (1) 19		

the increasing percentage of queenless nests as the season advances. No doubt sometimes the death of a queen results in death of the colony; presumably, however, she is sometimes if not normally replaced, as is regularly the case in nests of *L. rhytidophorum* (Miche-ner and Lange, 1958).

Efforts to shed light on these problems by marking queens in the spring when they are active as pollen collectors, in the hope of later digging them from the same nests and thus gathering data on their longevity, were failures year after year. This failure was due, in different instances, to loss of marking paint, the normal high colony mortality (Figure 4) and perhaps in other factors. The possibility exists that the queens are regularly shorter lived than we have indicated above. However, as shown in Figure 22, males are not pro-

TABLE XI.—Indices of Wear of Queens of *Lasioglossum inconspicuum* with Enlarged Ovaries. Except for April, data are given for each half month instead of on a monthly basis. The data for April were obtained in the last half of the month.

Index of wear	Number of queens (groups A and B)					
	April	May	June	July	August	September
5.....			1 1	1 2	2 5	1
4.....	8		2 7	8 7	4 3	1
3.....	7	4 3	4 1	3 2	4 1
2.....	13	10 2	2 2	2 3
1.....		11	1 2	1	1

duced in numbers until the last half of June. Therefore it seems clear that new queens to replace overwintered individuals would not be likely to function until late June or early July. Most likely they arise as occasion demands from late June on through the summer. Queenless nests are not rare in summer as shown in Figure 33. Many queenless colonies are certainly dying but others probably

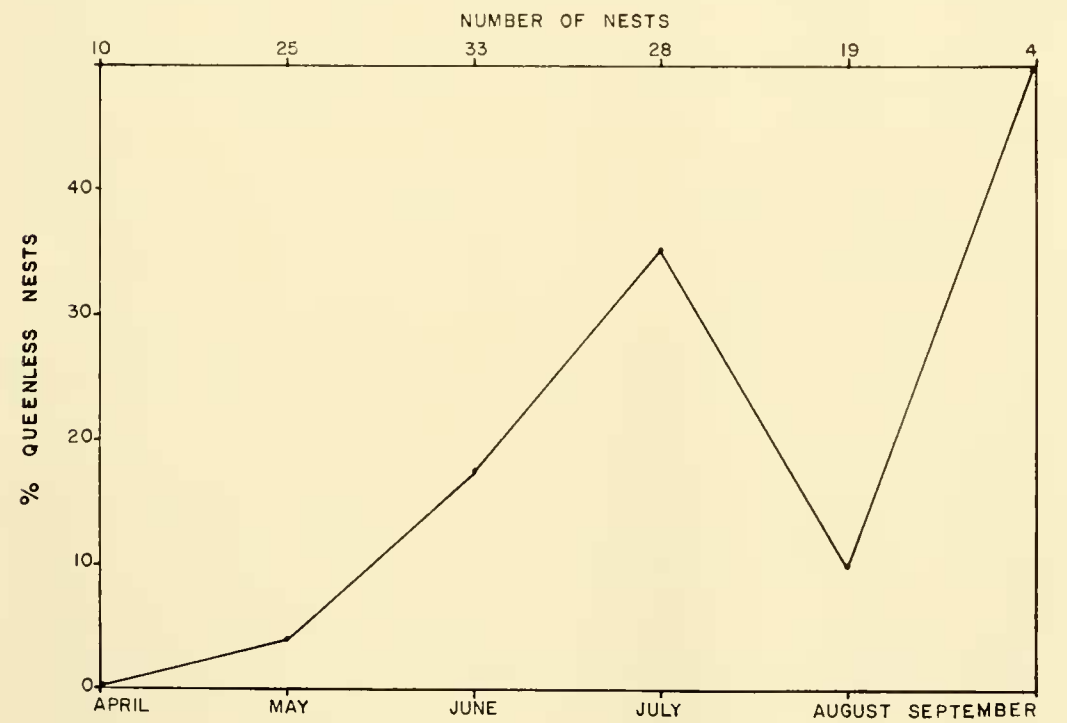


FIGURE 33. Graph showing the percentage of queenless nests in various months.

develop new queens. More specific data bearing on replacements of queens are as follows: On June 19, 1952, a nest (A) was opened that contained no queen except an unworn one of group B, with no eggs nearly ready to lay. There were neither eggs nor young larvae in the nest but there were one large larva, one prepupa, 15 female pupae and young adults still in their cells, and six unworn bees (group E) presumed to be workers. (Their wing lengths ranged from 3.04 mm. to 3.13 mm.; the queen's wing length was 3.27 mm.) During the following six days five other nests were opened; their queens were all old (indices of wear 4 and 5), of group A, and all but one of the nests had brood of all ages. It seems apparent that the original queen in nest A had been replaced, although the replacement had not yet laid her first egg, while in the other nests the overwintering queen was still active. From the above example one might suspect that group B queens are young ones developing toward the group A condition. Of course this is sometimes true but as Table X shows, group B individuals are often old and badly worn too.

Another interesting nest (B) was excavated on July 23, 1952. It contained brood of all ages and a probably overwintered, much worn (index of wear 4) queen of group A. It also contained another queen of group A and one of group B, both only slightly worn (index 2). Probably these were queens produced during the summer; possibly they replaced dead overwintered queens, but equally possibly they were additional queens. The nest also contained one fertilized worker (group D) (captured and marked as it left the nest on July 20, suggesting worker-like activities but not proving them) having one oocyte, .5 mm. long. Its index of wear was 3. In the nest also were two workers of group C and nine of group E.

On August 13, 1952, a nest (C) was opened. It contained two queens (group A) with indices of wear of 5. Possibly they were overwintered. In addition there was an individual of group D which, however, showed slight signs of general ovarian enlargement. Probably this was a young queen. In addition there were two anomalous individuals, among the half dozen summer specimens successfully dissected which were not placed in any one of the groups (A to E). They are probably best called fertilized workers but both had very irregularly enlarged ovaries. The enlargement involved chiefly one ovariole in each ovary, but the others were slightly enlarged; no oocyte approached the size or shape of a mature egg. One of these had an index of wear of 1, the other of 3. There were also 18 workers of group E.

In nest D excavated on June 24, 1954, which contained brood of all ages and three queens of group A (indices of wear 2, 4, and 4), there were also three unmated individuals included in group C. All were not or slightly worn (indices of wear 1, 1, and 2). They differed from ordinary individuals of group C in having all the ovarioles slightly enlarged, no oocyte greatly enlarged (largest .7 mm. long). They were larger than average workers (wing lengths 3.53 to 3.73 mm.). Possibly they were potential replacement queens. In addition there were thirteen probable workers of groups C and E (wing lengths 3.32 to 3.69 mm.). The largest of these was unworn and might have developed toward queenhood but one with a wing length of 3.64 mm. had an index of wear of 3.

Nest E, excavated on August 15, 1958, contained brood of various ages and one queen of group A (index of wear, 4). In addition it contained five workers. The latter had wing lengths ranging from 3.16 to 3.39 mm., while the queen was the same size as the largest worker. An additional bee was unworn with very slender ovaries; it was fertilized and therefore fell in group D. Its most remarkable feature was its size, only 2.84 mm. in wing length.

It is perhaps significant that most of the anomalous individuals discussed in the preceding paragraph occurred in nests containing relatively large populations and more than one queen. Perhaps whatever circumstances control the fate of a female function with less certainty in such nests, so that the anomalies discussed occur largely in such nests. It is obvious that such individuals are not characteristic of nests where the queen has died, leaving a group of workers some of which might in theory replace the queen functionally. Not a single caste anomaly was found in a queenless nest.

Workers: The three unworn young workers recorded for the month of May in Tables IX and X were all obtained on May 31. The number of the female bees that were classified as workers (groups C and E) is shown to fall between 77 and 86 percent for all of the summer months in Table IX. As is indicated in Table X, many of these bees which were called workers were unworn individuals that might in theory have developed into queens. That not many of those classified as group C or E in the summer months would have done so is indicated (1) by the small percentage of queens present in summer (2) by the fact that indices of wear for individuals of group E that have wing lengths less than 3.20 mm. and would therefore almost never become queens (Figure 31) average about the same as those of larger individuals that might become queens. If any large percentage of the larger individuals were being

removed from the worker class to become queens (so that they would be counted as workers only when young and unworn), the index of wear of the smaller ones classified as group E should average higher than that of the larger.

From the above it can be seen that classes A to E, while roughly comparable to similarly lettered classes of *L. rhytidophorum* (Michener and Lange, 1958), are not all identical in content. Classes A, B, and C are essentially alike for the two species. Class D as used in the present study includes overwintering females which were specifically excluded from that group in the study of *rhytidophorum*. They would have fallen in class D, however, had they not been dealt with in another way. Class E was limited by exclusion of unworn individuals in the study of *rhytidophorus*. This was necessary in order to get satisfactory data on workers because of the large percentage of queens and their presumably frequent replacement in *rhytidophorum*.

Unworn individuals placed in group E in September and October are no doubt mostly or all unmated queens that would become group D on mating.

Fertilized workers, while constituting a considerable percentage (nearly 8%) of the summer population of females of *L. rhytidophorum*, are nearly absent in *inconspicuum* during the summer. They would, of course, fall in group D. One such individual is discussed in the paragraph on nest B in the preceding section on "Queens," and one other was tentatively recognized during the summer. Of course such workers could be distinguished from young queens only if their activities were noted or if mandibular wear indicated considerable activity and age in a fertilized bee whose ovaries remained slender. Such bees were not found during the summer. In spring, however, some such bees were found as indicated in the section on "Division of Labor Among Queens in Polygynous Nests."

In September, however, fertilized workers appear in some numbers, as suggested by the high indices of wear of some individuals of group D, Table X. In a queenless nest excavated on September 17, 1952, four of eight workers were fertilized; one was unworn and might have overwintered as a queen but the others, having indices of wear of 2, 3, and 5, would not have overwintered, since overwintering bees are ordinarily unworn. On September 5, 1954, among specimens captured on flowers was one worker (out of six dissected) that was fertilized; it was collecting pollen like any field bee, and had an index of wear of 2. On September 15, 1954, five

workers (out of seven taken on flowers) were fertilized; they had indices of wear of 2 and 3. From these data one may summarize that in the late summer or fall, at the time that overwintering queens are being produced or probably shortly before, workers are produced which have certain queenlike characteristics, specifically willingness to mate. It is not surprising to find a physiological or behavioral continuum between workers and queens, since there is no clear differentiation in size or other characters either.

Two unfertilized workers were dissected and found to be anomalous for their unusual ovarian development. An individual which had ovaries like those of a group B queen but lacked sperm cells in the spermatheca was taken collecting pollen on flowers on August 5, 1954. It was classified as a group C worker. It was well worn (index of wear, 3) and quite small (wing length 3.39 mm.).

On August 23, 1954, a nest was excavated which contained brood of all ages except eggs. There were two queens of group A (indices of wear, 5) which had perhaps overwintered, and twelve workers (three group C, nine E). One of the workers (classified as group C) was peculiar in having ovaries like those of a queen of group A. Yet it was clearly unfertilized and was captured while entering the nest with a pollen load, indicating workerlike activities. This was the largest worker in the nest (wing length 3.55 mm.; others ranged from 3.21 to 3.42; the queens' wings measured 3.83 and 3.85 mm.) and had an index of wear of 4.

Since egg laying by workers is known to occur in queenless nests of *Apis* and *Bombus*, the question naturally arises as to whether workers of group C, and more especially those very unusual ones with much swollen ovaries such as described in the last two paragraphs, arise in nests which have lost their queens. The only unfertilized individual with much swollen ovaries taken from a nest was with two presumably functional queens (see preceding paragraph). As to ordinary workers of group C, one or more was found in each of 15 nests containing queens (groups A or B), and in only four nests lacking queens. It therefore seems clear that ovarian development of workers is not a result of lack of queens in the nest.

The importance of unfertilized egg-laying workers has been studied for halictine bees only by Noll (1931) who believed that most or all of the males develop from eggs of such workers. His evidence was very meager, however. No significant evidence on this matter was obtained in the present study.

Behavior of queens: Since most of the queens are produced in late summer or fall, we will discuss first the autumnal behavior of the young queens. Workers vanish entirely during September leaving the nests occupied by young queens. They do not maintain polished areas around the nest entrances, even if rain moistens the soil so that it would be easily worked. They commonly do maintain the nest entrances in their neat, constricted form, and on warm days at least as late as October 22 they are often to be seen guarding the nest with the head filling the hole, just as do guards at other seasons. We have not seen guarding in the few nests that were later found to contain only a single young queen.

During September and October both sexes may be seen sucking nectar from various flowers such as *Solidago* and especially *Aster*. Although males become less abundant on flowers as the season progresses, the young queens are sometimes very abundant on flowers in mid-October.

From October 19 to 22, 1952, by which time most of the flowers were dead, females of *L. inconspicuum* as well as other species of *Lasioglossum* were feeding on honeydew from the aphid, *Anoecia corni* Koch (determined by E. O. Essig). The bees were lapping the honeydew from the leaf surfaces of *Cornus asperifolia* on which the aphids were feeding. This was the only time that bees were seen feeding except from flowers.

By late October most of the nests become closed by rains and the bees remain inside. No nests were seen open in November. Excavation of nests in mid-November showed the overwintering queens at depths of 22 cm. and deeper. They were either in the main burrow, in short branches or in empty cells.

As indicated in the section on "Seasonal Cycle," young queens first reappear at the surface in late March or April. For a time many, at least, of them fly about and alight here and there on the soil as though looking for nesting places as described in the section on "Nest Construction." Such behavior may be seen as late as May 10, probably indicating diversity in the time when queens start their spring activity.

As already indicated, some of the queens remain in their overwintering nests and re-use them, while others establish new nests. (Observations on the manner of establishing new nests are described in the section on "Nest Construction.") Those which establish new nests do so as lone individuals while those remaining in old nests often are associated there with their sisters.

Lone queens do not make the smooth areas around their nest entrances which otherwise characterize nests of *L. inconspicuum*. Neither do lone queens appear as guards at their nest entrances. However, disturbance of the entrance with a hair or grass blade does sometimes cause a lone queen to come to the entrance, bite at the offending object, and even turn and plug the entrance with her abdomen as guards typically do (see section on "Guarding and Other Activities at the Nest Entrances"). One such queen was seen to keep a small mutillid out of her nest for an hour with her abdomen. Nests occupied in spring by two or more queens are often provided with smooth areas around the entrances, just as with the summer matrifilial colonies. In such cases guarding of the entrance occurs regularly. Workerlike activities of some queens in polygynous nests are suggested in the section on "Division of Labor among Queens in Polygynous Nests."

Because of variable (and often rainy) spring weather, the duration of the various phases of the spring activity of queens is variable. However, we have many data comparable to the following: Nest A, excavation started April 26, pollen still actively being collected on May 8, the nest closed and not recognizable on May 13, 18, and 25, reopened by one or more workers on June 1; Nest B, excavation started May 8, provisioning observed on May 13 and 15, nest closed and not recognizable on May 25 and June 8, open and at least one worker present on June 12. Such data show that after provisioning the last cell of the queen nest, the queen remains inactive in her nest for two or three weeks until the emergence of the first workers. This is an approach to the condition found in some Eurasian species in which the queen produces her offspring in discrete broods during the spring and summer (Noll 1931; Bonelli, 1948) or annually in the case of queens that live for several years (Plateaux-Quénu, 1959). In *L. inconspicuum* there is no evident cessation of activity of the queen after the appearance of the first workers in June until her summer or autumn senility.

After emergence of the workers and resumption of her activities, the queen never, so far as we know, acts as guard, nor does she collect pollen. Queens regularly have pollen as well as nectar in their crops, showing that they eat freely, as would be necessary considering their continued production of eggs. We have taken two queens (group A), one in July, one in early August, on flowers; both were apparently sucking nectar. We captured one queen (group A) as she was returning to her nest on July 21. From these data

we suspect that the queens leave the nests to feed. The paucity of such records (3 egg-laying queens out of 180 females captured in the field in June, July, and August and dissected) shows that the queens do not spend much time away from their nests and, furthermore, suggests that they may feed sometimes if not regularly on food brought to the nest by the workers. One group D female (probably a replacement queen) was taken on flowers in July.

That queens even after there are workers in their nests, continue to work with their mandibles, presumably in cell or burrow excavation, is shown by the increasing average indices of wear of queens as summer progresses (Tables X and XI). This increase is also one of the best evidences of longevity of many queens, although there is also evidence of production of new queens during the summer.

That much of the mandibular wear results from construction of cells and perhaps from the construction of the fine smooth cell lining is suggested by the fact that queens taken in April and May from old nests whose burrows were already made the previous year have mandibles just as worn as do queens that started new nests and had to dig their own burrows. Similarly for *Augochloropsis sparsilis* (Lepeletier) it was deduced by Michener and Lange (1959) that much of the mandibular wear results from cell construction. If this is true, the queens of *L. inconspicuum* probably are active in cell construction even when workers are present in the nest, since the queens' mandibles become more and more worn.

Division of Labor Among Queens in Polygynous Nests: In summer, when workers are present in the nests, we have no evidence of division of labor among queens in nests containing more than one queen. The degree of ovarian development of one queen in a nest has no obvious relation to that of another so that there may be, for example, in a digynous nest, two queens of group A, two of group B, or one A and one B.

In spring, when there are no workers, the queens in polygynous nests sometimes all have enlarged ovaries and, as Figure 18 indicates, all presumably lay eggs. Figure 18, however, is based on nests opened in May and especially in the later half of May; *i. e.*, on nests in which the production of new cells by the queens has stopped. Earlier in the spring most of the polygynous nests contain one or more "queens" that have slender ovaries (group D) or occasionally ovaries suggestive of those of workers of group C.

The fate of these overwintered individuals which are presumably potential queens is not clear. Presumably at least some of them

attain full ovarian development later. Some of them may leave their overwintering nests to establish their own new nests. However, we have repeated records of such bees collecting pollen and carrying pollen loads to their nest. Clearly in this case they are, for the time at least, functioning like workers in that they are provisioning cells in which other bees (queens of groups A and B) will lay eggs. It is probable also that it is such bees that guard the nests and make the smooth areas around the entrances since these are activities of workers in summer. It is therefore quite possible that some of the worker-like but fertilized overwintered females are short-lived like workers. Therefore their disappearance in late spring may result either from their death or from further ovarian development.

To give more completely our data on the ovarian conditions of females in polygynous nests opened in April and the first half of May, the conditions of females from such nests are indicated below in terms of groups (as defined in the section entitled "Caste Differences"), those from each nest being enclosed in separate parentheses: (AB) (AAB) (BB) (ABD) (ABD) (ABD) (AAD) (AABBDD) (BDD) (BD) (ADD) (AAAAD) (AAAD). Lone females were also occasionally in group D but the great majority of lone individuals were in groups A or B, so that most of the individuals of group D found in the spring were in the relatively few polygynous nests.

Behavior of Workers: As can be seen from Table X, the average index of wear of workers is much less than that of queens. This indicates that they do much less excavation or cell making per individual than do queens. Workers of group C have higher average indices of wear than those of group E, showing that they work more or longer in the nest than do those of group E. Individual workers of either group, however, have indices of wear as high as any queen, indicating that occasional workers do much work in the nests.

In the course of studying the duration of pollen-collecting trips by marked workers during the summer, data were also obtained on survival and other behavioral characteristics of these workers. In addition to marking foraging bees, we aspirated other bees from the nest entrances and marked them. We learned that, unlike foragers, such bees, when released, often could not find their way back to their nest. We concluded that they probably had not been out of the nest and had not learned the landmarks that would permit them to relocate their nest, and we developed a technique for re-introducing them to their nest through a glass tube after marking.

After all the bees that we could get from a nest had been marked, new ones usually appeared on succeeding days. These new workers were consistently found at the nest entrance or were sucked from the nest with an aspirator, but were not foragers. From this we concluded that the workers pass through a preforaging stage when they do not go out of the nest. During this stage they act as guards or move about in the burrow below the entrance. Bees examined in this stage have unworn mandibles, indicating that they do little or no excavating. The duration of the preforaging stage doubtless varies with temperature and other conditions. We have one record of a marked bee remaining in this stage for six days, but most bees marked as preforagers were foraging within four or five days or less; of course there is no certainty that they were captured and marked as soon as they might have been. However, in artificial glass nests in which pupae were placed, workers acted as guards during the same day that they left their natal cells.

In two experiments involving five bees, presumably young guards were transferred artificially to other nests and lived the rest of their lives there. The marked transferred preforagers were first seen as guards, later becoming foragers, and behaved throughout exactly as though they were in the proper nests. Foragers transferred to the wrong nests are not attacked so far as we know but leave the new nest and return to the proper one in a few minutes.

Several observations suggest that when the preforagers first leave the nest, they make feeding, not pollen-collecting, trips of long duration which are preceded by unusually long and elaborate orientation flights.

We have numerous records of the pollen-collecting activities of individual foragers lasting for eleven and twelve days, and one for fifteen days. Mandibular wear occurs during this stage, indicating that nest construction and foraging are more or less synchronous.

The data presented above suggest that after the worker bee leaves its natal cell it may live for about three weeks. We do have a record of one individual that was still in its nest 32 days after marking, but for at least the last ten days of this period it was the only worker in the nest and so far as we know did not leave the nest. It might well have lived longer than more active workers.

Guarding and Other Activities at the Nest Entrance: One of the noteworthy activities of worker bees (and queens in polygynous nests in the spring) is guarding. Such activity is characteristic of most or all halictine bees in which more than one individual occurs

in the same nest and is well developed in *L. inconspicuum*. Except at night and on unusually rainy days, each nest during the summer months is plugged most of the time by the head of a worker bee, which fits rather neatly into the constriction of the nest entrance. Disturbance of the guard by a fiber or grass blade, or by natural enemies such as mutillids or *Paralictus*, usually causes the guard to strike out repeatedly with open jaws at the offending object. If the disturbance continues, the guard bee turns and plugs the nest entrance firmly with the posterior two-thirds of the dorsum of the abdomen. The guard may remain in this position for a long time if the disturbance continues, for example, if a mutillid is trying to dislodge the guard. The guard braces herself very firmly in this position and one of the convenient ways to mark preforaging bees is to paint the marks on their abdomens when they hold this position. Of course when the guard is in this position, foraging bees can neither enter nor leave the nest.

Ordinarily, however, when the guard is in the usual position with head up and face flush with the soil surface, a bee flying toward the nest entrance appears to provide a stimulus that causes the guard to retreat, just before the returning bee lands, into the broader part of the burrow below the nest entrance. If two or more nests are close together, returning bees sometimes enter the wrong nest. So far as we know, no fighting occurs in such cases and the guard seems to show no ability to exclude foreign individuals of *L. inconspicuum*, which however soon leave the nest, as though they recognized their error. Guards have been seen to fight off *Paralictus*, possibly because they approached hesitatingly rather than rapidly like the *L. inconspicuum*. Guards also withdraw into the wider part of the burrow to allow departure of bees leaving the nest.

The aggressiveness of guards in defending the entrance clearly depends in part on their age. Young guards (*e. g.*, unmarked ones that appeared in nests after all other workers had been marked) are timid and often descend into the nest without blocking it with the abdomen. Guards with a day or two of experience are much more effective.

Occasionally after repeated disturbance a guard pushes earth up from beneath with the end of her abdomen and plugs the entrance. We noted particularly that this often happens when heavy rain falls on the nest.

During the middle parts of hot sunny days, guards are often not evident. A small disturbance at the nest entrances will bring them

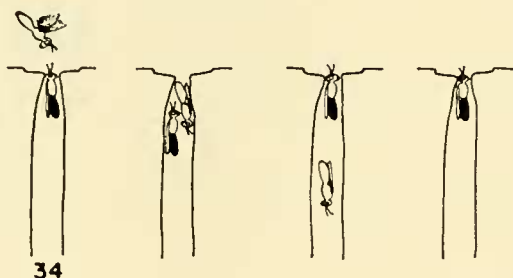
to the surface at such times, indicating that they are only a few millimeters below the entrances. Temporary shading of the nests by clouds or artificial means will also cause them to resume their positions at the surface on such days. It was found that if a thermometer resting on the soil surface registered above 125° F., the guards would not be visible at the nest entrances, but that if clouds or other shadows caused the temperature to drop to 120° F., the guards reappeared with their faces flush with the ground surface.

Guarding, as indicated previously, is largely an activity of preforaging workers although we have numerous records of a foraging bee spending some time as a guard, and as indicated previously, even queens may sometimes do so in the spring. Even a lone queen sometimes comes to the nest entrance at a small disturbance and may then turn and block the entrance with her abdomen, although such a queen never otherwise takes a position at the entrance as a guard. In nests containing several preforaging workers, each may take a turn as guard. We have seen such guards (marked for individual recognition) remaining at the nest entrance for periods ranging from 30 seconds to four hours, but perhaps one half to one hour is normal, after which the guard is replaced by another individual.

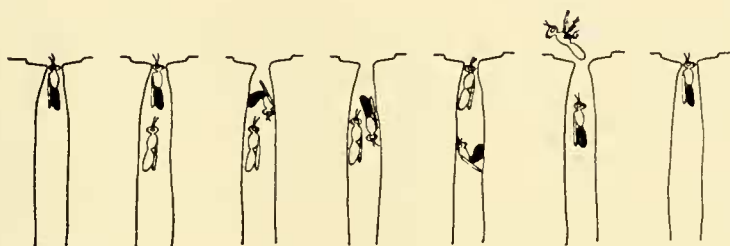
We were sometimes able to glimpse another bee below the guard when the latter allowed a forager to pass and were often able to suck with an aspirator a surprising number of bees from the nest entrance. To investigate the activities of bees below the nest entrances, we on various occasions and at various seasons dug a large excavation at the side of a nest and either put a piece of glass in such a position that it formed a window in the side of the upper two to four centimeters of the burrow or replaced the upper two to twenty centimeters of the burrow with a glass tube of the same diameter as the burrow. The bees came to and went from such modified nests in a normal manner providing the nest entrance proper was not destroyed and the soil on one side of the entrance was undisturbed. The observations described below were made in such situations but we have many bits of evidence indicating that they represent normal behavior. The bees in such nests were marked with colored paint for individual recognition. By making our excavation large enough to contain the observer's body, it was possible to place the eye or a lens very close to the bees themselves. Light was kept out of the glass walls of the burrows except when observations were being made.

At a nest entrance when only one bee was acting as guard, the

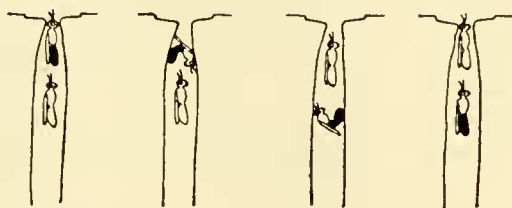
return of a bee from the field caused the activities shown in Figure 34. The departure of a bee to the field caused the activities shown in Figure 35. The turning of the guard shown in Figure 35 is invariable, so far as we know; bees always pass one another in the



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FIGURE 34. Diagrams showing how a guard draws into the burrow, behind the narrow entrance, to allow a returning bee to pass. The guard is marked with black on the abdomen.

FIGURE 35. Diagrams showing how a foraging bee passes the guard when leaving the nest. Note that the guard backs into the burrow, away from the narrow entrance, and then turns over so that the bees face one another when passing. The guard is marked with black on the abdomen.

FIGURE 36. Diagrams showing how two guard bees exchange positions. One of them is marked with black on the abdomen.

FIGURE 37. Diagrams showing activities of three guard bees (differentially marked for easy recognition) during five minutes of observation. No foragers left or returned during this period. Note that the bees sometimes turn over for unknown reasons other than to allow passing.

burrow when facing toward one another and not when facing in the same direction.

In most active nests which we studied in summer there were two or more bees spending much of their time at or near the nest entrance. If the guard were removed artificially, another bee usually replaced it immediately, for it had only to ascend to the nest entrance from a few millimeters below. The same thing can be repeated several times in nests with large populations of young workers; after the supply of young workers is exhausted it seems to take longer for the older workers to find the unguarded nest entrance and take up positions as guards.

In view of the above it was not surprising to find that several workers (usually young ones) often are in the upper part of the nest burrow. They sometimes exchange positions as guards, as indicated in Figure 36; again they pass only when facing one another. Often there is much moving up and down the burrow by bees below the guard, and a bee often turns over and over, summersault fashion, even when not passing another bee. Figure 37 shows the activities of three bees in the upper part of the nest burrow; the entire series of sketches represents a period of about five minutes of observation. Of course when a bee that is leaving the nest comes up the burrow, each of the bees above it must turn over in order to pass, as is shown for a single bee in Figure 35.

Co-operative Activity Among Workers: Division of labor among workers of various ages has already been described, younger individuals remaining in the nest and often acting as guards, older individuals serving as foragers, and sometimes also as guards. The present section presents evidence on co-operative activity among foraging workers. It is, of course, possible that each worker makes and provisions its own cells; illustrations such as Figure 14 show that each worker does not make its own branch burrow and group of cells, for there are not enough such groups. Alternatively, the workers might co-operate in making and provisioning cells, several working on one cell simultaneously.

Tentatively, we believe that such co-operative activity occurs, at least in provisioning. The number of pollen-collecting bees in a nest appears to consistently exceed the number of cells being provisioned. For example, one nest, watched continually in the morning hours, yielded four pollen collectors; on excavation in the afternoon of the same day only one partly-provisioned cell was found, plus two empty cells which the pollen collectors might theoretically have started to

provision with the pollen that they were carrying when captured. Another nest yielded seven pollen collectors; when excavated the same afternoon three partially-provisioned and four empty cells were found. A third nest yielded twelve pollen collectors; when excavated the same day two partially provisioned cells, five empty cells and two complete pollen balls in open cells without eggs were found. Such data seems to leave no doubt of co-operative activity in provisioning cells, but unfortunately we often felt that because of the extent of the nest, small size of the burrows, and often poor soil consistency, we might have missed a few cells. We do not believe that such was regularly the case, however.

A further effort to prove more decisively that workers co-operate in provisioning cells was made by marking pollen loads of returning foragers with colored powders, using different colors on different foragers which were marked for individual recognition. This proved to be a difficult technique for the foragers were much disturbed if captured; instead we blew the powder onto them just before they entered the burrow. We did find differently colored particles mixed in single pollen masses but always in such proportion that one greatly predominated and the others might have been introduced accidentally by bees that became contaminated in the burrow with powder lost from the bodies of other bees. We believe that the method may have some value for use with other species but regard it as inconclusive for such small and inconvenient forms as *L. inconspicuum*.

NEED FOR FURTHER STUDY

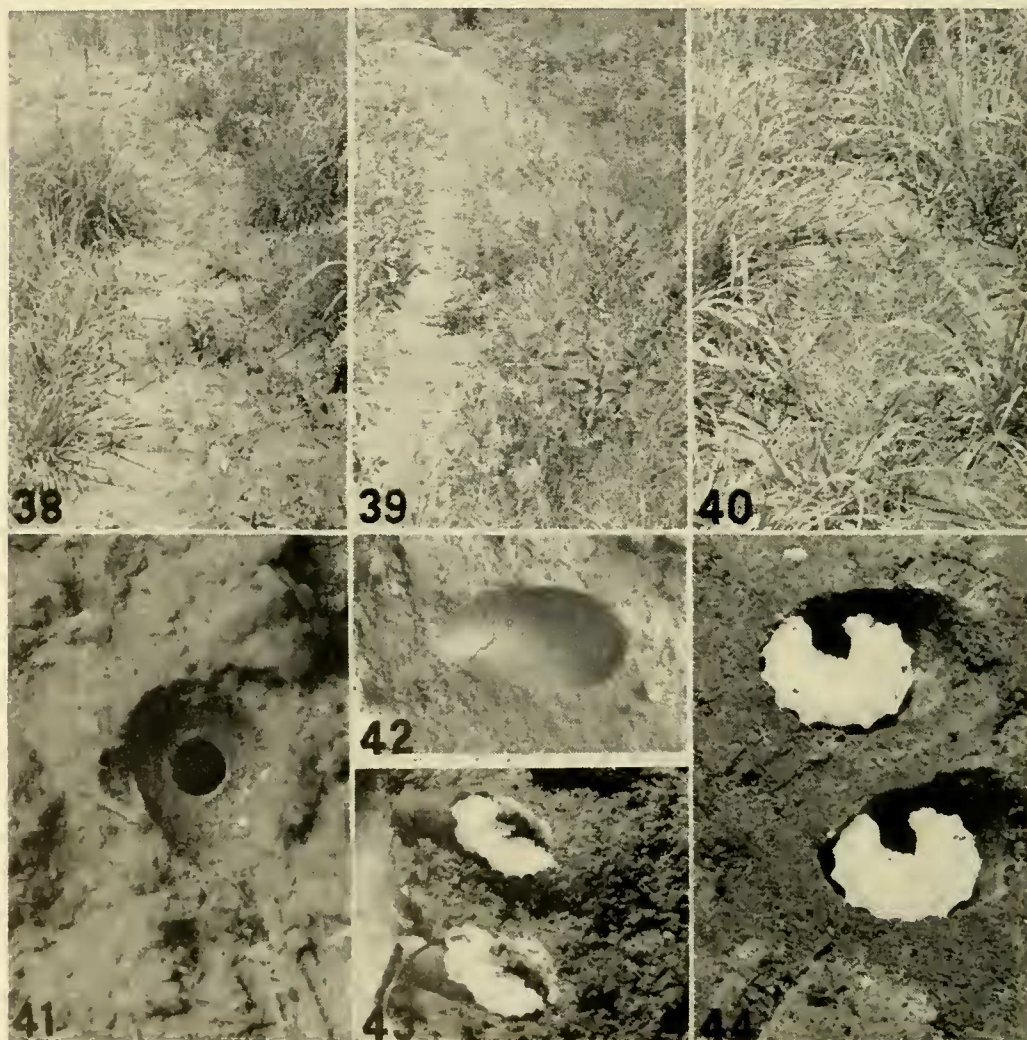
To the authors an impressive part of this study has been the enormous areas of investigation in which little or nothing is known (for this bee or for any other) in spite of a fairly intensive study. Some of these matters can be solved by additional field investigations. For example, whatever combination of temperature, light intensity, wind, and perhaps other factors determines when bees fly and when they do not could be elucidated by more field data, as could flight ranges, soil moisture requirements for survival of a colony, etc.

However, for investigation of many of the more basic aspects of social organization, our techniques have enabled us to do little more than hint at possible solutions to the problems. It is urgent that techniques be developed so that actual behavior in the nests can be seen rather than merely inferred. We need to know more about integration of members of the colony, the food sources of the queens

in matrifilial colonies (her own trips to the field, or food brought in by workers), the longevity of queens, the interactions among workers which are jointly provisioning cells, etc.

Obviously many interesting ethological observations could also be made if laboratory colonies could be established.

Another field in which more information is needed concerns the question of why some females become long-lived, sexually functional queens while others become short-lived workers. In the better known social insects the answers to this and related questions are partly known, but in primitively social insects such as *L. incon-*



FIGURES 38 to 40. Nesting places. Figure 38, Sycamore Slope; Figure 39, Prairie Road; Figure 40, Intersection.

FIGURE 41. Nest entrance, showing smooth depressed area.

FIGURE 42. Horizontal section of a cell. The scale at the bottom of the figure is in millimeters.

FIGURE 43. Pupae in cells; feces (pale) on upper distal surfaces of cells.

FIGURE 44. Prepupae in cells. The cut through both cells is oblique so that the feces scarcely show and the cell plugs are represented by only a little loose dirt at the right-hand end of each cell.

spicuum, they are quite unknown. Since caste is related to size, and size seems to be related to season (perhaps to temperature, probably not to kind of food as various acceptable pollen sources are available at all seasons), it would be interesting to rear bees under various temperature conditions (as well as with various amounts of food) and observe the behavior of the resulting adults. On the other hand, since workerlike activity can arise among presumably potential queens in polygynous spring nests, it would appear that caste determination can occur in the adult stage (as has been suggested also for *L. rhytidophorum* (Michener and Lange, 1958). If this is true, an interaction of some sort among females must be postulated, with pheromones or some other factor determining ovarian development, mating, longevity, etc. This seems unlikely among insects which seem to have so little contact with one another as members of a colony of *Lasioglossum*. Obviously an experimental approach to such problems is needed.

We have good hopes that it will soon be possible to colonize this or other halictine bees in the laboratory and that having achieved this, some of the questions enumerated above can be answered.

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